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JOSEPH CHARLES ARTHUR (1850-1942)

EDWIN B. MAINS (WITH PORTRAIT)

Joseph Charles Arthur was born at Lowville, New York, January 11,*1850. At the age of six, he moved with his parents Charles and Ann Arthur to Charles City, Iowa. Here he attended country school and developed an interest in plants which continued throughout his long life. When Iowa State College opened in 1869 he was one of the first students, receiving his botanical training under Professor C. E. Bessey. He graduated with the degree of B.S. in 1872. He returned to Iowa State College in 1876 and received the degree of M.S. the following year. He later studied at Johns Hopkins (1879) and Harvard (1879). In 1886 he was granted the D.Sc. from Cornell University. He received the degree of LL.D. from the University of Iowa in 1916 and D.Sc. from Iowa State College in 1920 and from Purdue University in 1931.

His professional career started at Iowa State College where he was an instructor from 1876 to 1878. Apparently his association with E. W. D. Holway began at this time. This continued for 48 years until Mr. Holway's death in 1923. Mr. Holway's collections of rusts added much toward the completeness of Dr. Arthur's studies, specially for the Tropical American Uredinales. In 1876 Dr. Arthur published his first scientific paper, a catalogue of the flowering plants of Iowa. He also

¹ Contributions to the flora of Iowa; a catalogue of the phaenogamous plants. 43 pp. Charles City, Iowa, 1876.

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exhibited an herbarium of Iowa plants at the Centennial Exhibition in Philadelphia in 1876, receiving a bronze medal.

After serving as an instructor at the University of Wisconsin (1879–1881) and at the University of Minnesota (1882), he was appointed Botanist at the New York Agricultural Experiment Station, Geneva, New York. His was the first appointment to such a position in this country. At Geneva he was mainly concerned with investigations of plant diseases with special emphasis on pear blight. In the mycological field he published a paper ² concerning a species of *Entomophthora*.

In 1887, he accepted the position of Professor of Botany at Purdue University and the following year became Professor of Vegetable Physiology and Pathology and Botanist in the Purdue University Agricultural Experiment Station. As such he continued until his retirement in 1915 as Professor Emeritus of Botany. In 1901 he married Emily Stiles Potter of Lafayette, Indiana, who died in 1935.

Throughout his life Dr. Arthur was an indefatigable investigator and writer in the fields of physiology, pathology and mycology. In addition to publishing a number of papers concerning the physiology of plants he exhibited apparatus of original design at the Columbian Exposition in Chicago in 1893. He was among the pioneers in plant pathology, his most important contribution being the use of formaldehyde as a fungicide, specially for the scab of potatoes.

In the mycological field he was early recognized as an authority for the Uredinales. His first paper ³ concerning the group was published in 1883. For many years after his retirement in 1915 he continued his rust studies. His last publication was the "Manual of the Rusts of the United States and Canada" (1934). Thus for over half a century he added to the knowledge of the Uredinales, contributing more than 100 articles to botanical journals and publishing three major publications.⁴

A new larval Entomophthora. Bot. Gaz. 11: 14-16. 1886.

³ The interpretation of Schweinitzian and other early descriptions. Am. Nat. p. 77-78. 1883.

⁶ Uredinales. N. Am. Flora 7: 83-969. 1907-1931. Plant rusts, in collaboration with F. D. Kern, C. R. Orton, F. D. Fromme, H. S. Jackson, E. B. Mains, G. R. Bisby. 446 pp. 1929. Manual of the rusts in United States and Canada. Illustrations by George B. Cummins. 438 pp. 1934.

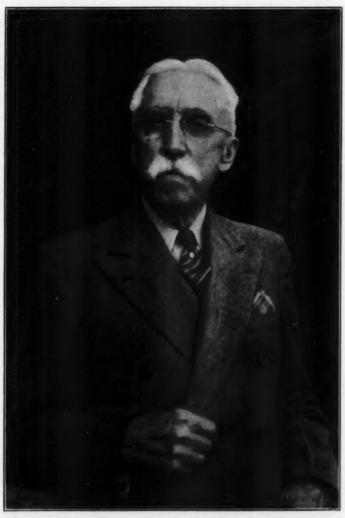


Fig. 1. Joseph Charles Arthur. (Photograph by George F. Weber, Nov. 24, 1937.)

With the establishment of a plan for the publication of a Flora of North America by the New York Botanical Garden, Dr. Arthur assumed the responsibility of providing a complete taxonomic treatment of the Uredinales. The first number was published in 1907. After his retirement, support for the study was continued by the Purdue Agricultural Experiment Station and the last number was completed in 1931.

He was early faced with the multiplicity of names and difficulties in establishing species concepts. Little was known concerning the heteroecism of North American species. This necessitated field studies to establish the association of alternate hosts, involving extensive trips throughout the United States. He was also aided by many correspondents who furnished additional information and collections. For nineteen years, May and June were busy months in the laboratory at Purdue. With the help of a special assistant, overwintered collections of teliospores were tested for germination and cultures were attempted on selected hosts. The routine was relieved by the excitement attending the first demonstration of a new connection. The results of these studies were published yearly and they were summarized by Dr. Arthur in 1921.

In these studies of host relationships he was soon confronted with the problem of host specialization in relation to the species concept. He finally concluded that "morphological characters must be the final test for the species." This emphasis on morphology resulted in the employment of characters which had received little or no use previously, specially the number and arrangement of germpores in the spores.

The importance given to the pycnium (spermagonium) and the stages with which it was associated resulted in the employment of life cycles in the delimitation of genera with a considerable multiplication of genera in the treatment in the North American Flora. This did not find general acceptance and was finally abandoned in the Manual of Rusts for North America. However, there resulted a better understanding of the life cycles of species. Another result was the proposal of a more usable terminology of the various spore stages which has found general acceptance in North America.

⁶ Mycologia 13: 12-23; 230-262. 1921.

An herbarium of 60,000 specimens of rusts was developed. Comparison of collections was facilitated through the use of a uniform system for drawings and notes. This herbarium in the Botany Department of the Agricultural Experiment Station of Purdue University has been designated the Arthur Herbarium.

Dr. Arthur was a member of Sigma Xi, Phi Kappa Phi, Societe Mycologique de France (1884-1889), Association Internationale des Botanistes (1901-1915), Deutsche Botanische Gesellschaft, Society for Promotion of Agricultural Science (1886-1920), Botanical Society of America, American Mycological Society (1903-1906), Torrey Botanical Club, Washington Academy of Science (1905-1912). Plant World Association (1907-1919). American Phytopathological Society, American Association of University Professors, American Philosophical Society, American Society of Naturalists, Mycological Society of America and corresponding member of the Academy of Natural Science of Philadelphia. He was a fellow of the American Association for the Advancement of Science, the Indiana Academy of Science and the American Academy of Arts and Science and honorary fellow of the Iowa Academy of Science. He was elected vice-president (1897), and president (1901 and 1919) of the Botanical Society of America; president of the American Phytopathological Society (1933); president of the Indiana Academy of Science (1892); assistant general secretary of the American Association for the Advancement of Science (1887) of which he was also secretary of section F in 1886 and vice-president of section G in 1895. He served as associate editor (1883-1885; 1900-1904) and editor (1886-1900) of the Botanical Gazette and associate editor of Mycologia (1909-1932). He was one of the organizers and secretary of the Madison Botanical Congress in 1893 and a delegate to the International Botanical Congress at Vienna in 1905 and at Brussels in 1910.

Dr. Arthur died at Brook, Indiana, April 30, 1942, and was buried at Lafayette, Indiana. It is given to few men to have such a long active life. His scientific achievements will serve as an everlasting monument.

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DISTRIBUTION PATTERNS IN MELAMPSORELLA IN THE NATIONAL FORESTS AND PARKS OF THE WESTERN STATES¹

S. M. PADY (WITH 3 FIGURES)

Melampsorella is the cause of a witches' broom rust disease on various species of Picea and Abies. Although the disease has long been known due to its conspicuous appearance and wide distribution, considerable confusion exists at present as to the number of species. Earlier investigators (3) described two species under the form genus Peridermium, one species on Abies, the other on Picea. Subsequent workers, among them Rhoads et al (7), subscribed to this concept. Arthur (2) has recently considered the genus to be monotypic basing his conception on the character of the pycnia which he considers to be subcuticular in both forms. In 1939 the writer made a comparative study (5) of infections on Abies and Picea, particularly with reference to the pycnia, and discovered that they are distinctly different, being subcuticular and flattened on Abies as earlier reported (4), but subepidermal, actually substomatal and spherical, on Picea. These differences, plus others among which may be mentioned the size, color, markings, and date of maturity of the aeciospores, and the size and manner of growth of the witches' brooms, have convinced the writer that there are two species of this rust. In a later paper (6) additional information was obtained on the nature of the substomatal pycnia from a study of fresh material and from specimens in the Arthur Herbarium, and further evidence was presented in support of this conclusion. This paper presents the results of studies made during the summer of 1941 on the distribution patterns of these two species, as well as evidence based on field observations and collections.

¹ With the support of a grant from the Penrose Fund of the American Philosophical Society.

In the Gothic area of Colorado previously studied (5, 6) infections were very numerous on Picea vet scarce on Abies, notwithstanding the fact that the latter occurred abundantly throughout the region. It was suspected that if such differences occurred in other areas it might constitute further evidence for the delimitation of the two species. Localities were selected for detailed study on the basis of the presence of the hosts and the rust. Data on the distribution of the disease were obtained from specimens in the Arthur Herbarium at Purdue University and from a list of the specimens in the Forest Pathology Herbarium, Bureau of Plant Industry, Washington, D. C.,2 and from correspondence with officials of the National Parks and National Forests.3 Data on the distribution of the Picea and Abies species were obtained from various sources, mainly from Bailey's "The Cultivated Conifers" and Munn's maps of the distribution of forest trees (U.S.D.A., M.P. 287). Numerous collections (Table I) and many detailed observations were made in these areas. It was found that the two species differed in their distribution and two distinct distribution patterns were obtained (Table II and FIG. 1). A brief description of the situation in each area is given below.

UINTAH NATIONAL FOREST, UTAH

In the Uintah N.F. north of Hanna, along Wolf Creek on Highway 53, Melampsorella occurs abundantly on Abies lasiocarpa, some areas being very heavily infected. In one area, for example, over 250 witches' brooms were counted on Abies and only 6 were found on Picea, 3 of these being dead. Practically every tree had one or more brooms upon it and one large tree had over 30. One tree 7' tall, base 4" diameter, had 4 witches' brooms, 3 being dead, one terminal broom surrounding the trunk, and checking normal growth. The brooms were of all sizes, the larger ones being very conspicuous. New growth was just beginning and the pale yellowish green young leaves gave the brooms a yellowish cast in striking contrast with the normal dark

² The assistance of Dr. R. Kent Beattie in preparing the list and for his many helpful suggestions is gratefully acknowledged.

⁸ The success of the trip was due in large measure to the excellent coöperation of these officials. Their assistance was greatly appreciated.

TABLE I

Record of Collections of Melampsorella in the National Forests
and Parks in 1941

Date		Host	Col- lec- tions	Locality		
June	13th Picea pungens 14th Abies lasiocarpa Picea Engelmanni		4 2 1 1	Uintah N.F., Utah Wasatch N.F., Utah	Wolf Creek, N. of Hanna Trail to Alexander Lake Provo River	
64 66	17th 19th	Pices pungens	5 3 1	Powell N.F., Utah Grand Canyon N.P., Aris, Kaibab N.F., Aris,	E. of Widtsoe Along North Rim Southern Border	
July	3rd 12th	Abies magnifica A. magnifica var. shastensis	1	Yosemite N.P., Calif. Crater Lake N.P., Ore.	Washburn Pt. and vicinity 2 mi. E. of Headquarters	
66	15th 17th	Abies amabilis Picea Engelmanni	1	Mt. Hood N.F., Ore. Mt. Rainier N.P., Wash.	Below Timberline Lodge Trail to Emmons Glacier	
44	23rd	Abies lasiocarpa	2	Glacier N.P., Mont.	Vicinity of Logan Pass	
65	25th	Picea glauca Picea Engelmanni	1	Blackfeet Indian Res., Mont. Yellowstone N.P., Wyo.	10 mi. S. of St. Marys Artists' Point	
88	66	Abies lasiocarpa	3 5	64 64 69	Mt. Washburn and vicinity	
66	" 26th	Picea pungens Picea Engelmanni	2 3	46 46 45 45 45	Mammoth Hot Springs and vicinity	
66 05	27th	Abies lasiocarpa	1	41 44	Firehole River and vicinity	
66	64	Picea Engelmanni	1	64 65 65	Yellowstone Lake and vicinity	
66	28th	Picea pungens Abies lasiocarpa	2	Teton N.F., Wyo.	S, of Yellowstone Park	
66	96	44 44	2	Grand Teton N.P., "	Jenny Lake	
64	20th	Picea Engelmanni Abies lasiocarpa	1	Wyoming-N.F., Wyo.	Hoback Canyon	
88	30th	Picea Engelmanni Picea pungens	4 2	Medicine Bow N.F., Wyo.	Libby Flats and vicinity	
55 A	1st	Abies lasiocarpa	3	** ** ** **	Albany and Mullen Creek	
Aug.	44	Picea Engelmanni Abies lasiocarpa	6	45 45 46 46	Battle Lake and vicinity	
64	3rd	P. glaucs var. albertiana	4	Black Hills N.F., S. D.	West of Pactola	
46	**	P. glaucs var. albertiana	1	Harney N.F., S. D.	N. of Custer	
		Total	75			

green foliage. The infected buds were also greatly advanced over normal buds which did not as yet show any growth. At higher altitudes around 9000' the brooms were still dormant, but at lower altitudes the infected branches were ½" long.

Pycnia were present on the closely packed leaves but mature pycnia were found only on the exposed portion of the leaf. Except for the stomatal areas which do not bear them, the pycnia are scattered over the leaf being most numerous at the tip. A peculiar feature of the pycnial stage on *Abies* was a very pronounced disagreeable odor; the pycnia on *Picea* did not give off any odor that was particularly apparent. While the possible function of the odor remains a matter of conjecture it does emphasize a further point of difference in the two species.

TABLE II

Collections and Detailed Observations of Melampsorella in the National Forests and Parks in 1941

	ON PICEA			On Abres		
Locality	Col.	Det. Ob.	Comments	Col.	Det. Ob.	Comments
Uintah N.F., Utah		2	B		10	
Wolf Creek, N. of Hanna	_	-	Rare Few, scattered	4	10	Moderately heavy Abundant
Wasatch N.F., Utah Trail to Alexander Lake Along Provo River	2	2 2	Scattered Abundant	1	2	Light, scattered Few
Powell N.F., Utah E. of Widtson	5	20	Very heavy		F	ost absent
Grand Canyon N.P., Ariz. Along N. Rim.	3	33	Heavy	_	_	and the state of t
Kaibab N.F., Aris. Southern Border	1	2	Seattered	_	_	
Sequoia N.P., Calif. Halstead Creek		-	ost absent	_	5	Light
Yosemite N.P., Calif. Washburn Point and vicinity			ost absent	2	13	Heavy in this area
Crater Lake N.P., Ore.		H	ost absent	1	1	Rare, one infection
Mt. Hood N.F., Ore. Below Timberline Lodge		Н	ost absent	1	6	Light
Mt. Rainier N.P., Wash. Trail to Emmons Glacier		3	Light	_	_	
Glacier N.P., Mont, H'way E, and W, of Logan Pass		10	Heavy	2	3	Moderate
Plackfeet Indian Reservation, Mont. 10 mi. S. of St. Marys		1		_	_	
Yellowstone N.P., Wyo, Artists' Point and vicinity	1	1	Uncommon	3	6	Heavy
Mt. Washburn and vicinity Mammoth Hot Springs and vicinity	2	1 2	Fairly abundant Abundant	5	4	Moderately heavy
Madison Jet, and vicinity	3	3 2	Very heavy Heavy	_		
Vicinity of Old Faithful. Yellowstone Lake, W, shore	3	6	Epidemic	1	2	Light
Teton N.F., Wyo. Road S. Yellowstone Park	_	_		1	1	Numerous
Jenny Lake		_		2	3	Light, scattered
Wanning N F Wan	1	1	Moderately heavy	1	1	Light
Hoback Canyon Med icine Bow N.F., Wyo. Univ. of Wyo. Camp and vicinity	3.	2	Heavy	1	2	Light
Liddy Flats	1	3 2	Light Abundant	1	1	Heavy
Upper Nash Fork Camp Ground Albany and Keystone and vicinity		2	Heavy	1	1	Light Scattered
Mullen Creek and vicinity	-	2	Fairly abundant	-	-	Domestica ou
N. Mullen Creek	2	3	Fairly abundant	1900	-	
Vicinity Encampment	-	1	Light	1	2	Moderate
Vicinity Battle Lake	-			4	7	Epidemic
Soapstone Ranger Station	-	-		1	1	Light
Black Hills N.F., S. D. Black Fox Camp Ground and vicinity Deerfield Camp Ground and vicinity	3	5	Heavy Moderate	Host absent Host absent		
Harney N.F., S. D.	1	4	Heavy		H	lost absent

The witches' brooms of the species on *Abies* are typically compact with a dense growth of many small branches, somewhat spherical, often rather symmetrical, and rarely exceeding a diameter of 2'-3'. The infected leaves are deciduous but are not usually cast until the spring; during the winter they become dark

in color and somewhat shrivelled, which with the bare older branches, give the entire broom a dark somewhat lifeless appearance during the dormant season. The gall is prominent especially when the broom is located on a young branch.

The witches' brooms of the species on *Picea* are extremely irregular, the terminal bud growing much more rapidly than the lateral buds, which results in a larger more diffuse type of broom. Sometimes long pendant branches are found on these brooms. The infected branches are pale brown in color and thus the dormant brooms are usually paler than those on *Abies*.

The infected branches of both species sometimes display marked changes in geotropism. The normal branches are transversely geotropic while the infected branches tend to be negatively geotropic. In some cases the entire broom has been found growing at right angles to the lateral branch on which it is located.

In the vicinity of Wolf Creek Summit and along Highway 53 further west, many infections were observed on Abies, few on Picea; those on the former were all dense, compact, many being dead. In this entire region both hosts were abundant but the species of Melampsorella on Abies is clearly dominant, a situation found to exist throughout this region.

WASATCH NATIONAL FOREST, UTAH

Along Provo River, east of Kamas, and in the Provo River Canyon, witches' brooms were not especially abundant. Infections on both hosts were scattered and occurred as single usually isolated infections. In one area the *Picea* form was fairly abundant. In this region infections were not heavy enough to justify any conclusions, although it would seem to indicate that the form on *Picea* is most numerous and tends to be dominant. It is interesting to note the different situation here, although only a few miles from the Uintah area.

POWELL NATIONAL FOREST, UTAH

Driving east from Widtsoe, Utah, along the road to Escalante one encounters a densely forested area in which Melampsorella

is very abundant on Picea pungens, the only host that grows here. This area begins 41/2 miles from Widstoe and continues for almost two miles. Infections were heavy, the brooms generally large and conspicuous, often reaching a diameter of 4'-6'. As is typical of the species on Picea many of the brooms were very irregular; one broom for example completely surrounded the main trunk of a large tree, extending from the base upward to a distance of 6'. The size of the witches' brooms was extremely variable, infections being found in all stages of growth. On one small tree 19' high the broom was terminal, forming a dense irregular mass at the top of the tree; the broom was dead and the tree was dving. In one other similar case the terminal bud of the trunk had become infected checking further growth. but a lateral bud had grown up around the broom to continue the normal growth of the tree. There was evidence in this area of considerable damage to the trees; one large tree with a base 2' in diameter had a mass of infected branches 20' from the top, the mass was 10' × 6' in diameter and was dead, as was the trunk from that point upward, suggesting that the infection had killed the tree.

Witches' brooms were found on all parts of the tree, the most conspicuous being those which occurred high up either on the main trunk or on lateral branches where the infected mass stood out clearly against the sky. Of the brooms studied, 2 were terminal on the main trunk, 9 were found at various points along the trunk, 1 was terminal at the end of a lateral branch, 2 were located on a lateral branch, and 1 was found at the junction of a lateral branch and the main trunk. The large number of main trunk infections recorded is probably due to the fact these were so conspicuous that more of them were noted.

The infected buds were emerging much in advance of the normal buds which showed little or no growth, while the infected branches were $\frac{1}{4}"-\frac{1}{2}"$ in length. An examination of the pycnia shows they differ greatly from those previously noted on *Abies*; in appearance being darker and smaller, in distribution being confined to the stomatal rows on the four sides of the leaf, and also in the absence of any apparent odor.

GRAND CANYON NATIONAL PARK, ARIZONA

In the heavily forested region of the North Rim of the Grand Canyon National Park, Melampsorella was found abundantly on Picea pungens. Abies concolor is present there also but no infections were found upon it. One of the outstanding characteristics of infections found in this area was the large size attained by some of the witches' brooms, a large number of them reaching a diameter of 8'; one of the largest measured $10' \times 6' \times 5'$. The irregularity of many of these larger brooms plus the fact that some of them are partially dead, suggests that coalescence of two or more adjacent brooms may have taken place. The rapidly growing diffuse type of broom found on Picea would enable this to take place rather readily.

Several cases were observed where large trees had been snapped off at a point where the main trunk was infected. One such tree, broken 30' from the ground, bore a large irregular mass of infected branches at the point of breakage, and more than 20 witches' brooms of all sizes were scattered over the remainder of the tree, many of them dead. The broken top of the tree also had several brooms on it. The suggestion was very strong that the trunk infections had weakened the tree to such an extent that it was susceptible to breakage, caused possibly by high winds.

There were numerous trees here which were dead or partially dead, the result presumably of heavy infection since there were many dead or partially dead witches' brooms on the same tree. Young trees as a general rule were living even though heavily infected. One tree, 5' high with a basal diameter of 3", had a broom 12" × 16" surrounding the trunk at the base. Since both the host and parasite were approximately the same age it was evident that infection had taken place during the seedling stage. Each year as the broom becomes larger and larger the demands made upon the host are correspondingly greater, the result being the premature death of the tree.

This area demonstrates very clearly the different distribution patterns of the two species of *Melampsorella* since both *Picea* and *Abies* are present here in abundance, although infections are found only on the former. Conditions in this area were not only

favorable for infection since brooms of all sizes were found on both young and old trees, but were also favorable for the growth of *Picea pungens* and many of the trees grew to a great size. The largest and most conspicuous witches' brooms encountered during the summer's collecting were found in this area.

KAIBAB NATIONAL FOREST, ARIZONA

In this National Forest infections were found only at the southern extremity in a small area immediately bordering the Grand Canyon National Park. The total number of witches' brooms found in this region was 10, all being on *Picea pungens*; none were found on *Abies*, although *A. concolor* was present.

SEQUOIA NATIONAL PARK, CALIFORNIA

Along the western coast *Melampsorella* does not occur very heavily in any one locality. Most of the infections found were scattered and often difficult to find. In the Sequoia National Park, for example, a search was made for this rust and it was located in only one locality, about 10 miles from the Giant Forest in the region of Halstead Creek, where a total of 5 witches' brooms were observed at scattered points, all on *Abies magnifica*. Although the trees were very tall and the brooms inaccessible their bright yellow color made them conspicuous and the dense compact type of growth was readily observed. The mistletoe brooms on the same host frequently had a superficial resemblance to *Melampsorella*, due to the fact that the mistletoe is yellow in color and also stimulates the production of adventitious branches. There are no species of *Picea* growing in this region.

YOSEMITE NATIONAL PARK, CALIFORNIA

The disease was found abundantly in only one area in the Park, on Abies magnifica along the road to Glacier Point in the vicinity of Washburn Point. As in Sequoia National Park, mistletoe was very abundant and conspicuous and care had to be taken in determining the nature of some of the larger brooms which were not accessible for close observation. Melampsorella, however, may be readily distinguished from the mistletoe by the fact that the infected leaves are etiolated and the branches bear

only the season's leaves, while in the mistletoe broom the leaves are normal and are retained for several years. The yellow color of this broom is due to the yellow color of the mistletoe itself. Most of the infected branches of *Melampsorella* had attained a growth of 1½"-2" and were bright yellow in color, and hence

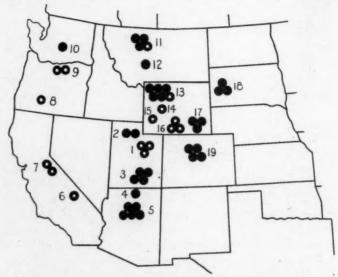


Fig. 1. The distribution patterns of the species of *Melampsorella*. The solid circles represent areas where the species on *Picea* is dominant; hollow circles represent areas where the species on *Abies* appears to be dominant. 1, Uintah National Forest, Utah; 2, Wasatch N. F., Utah; 3, Powell N. F., Utah; 4, Kaibab N. F., Ariz.; 5, Grand Canyon National Park, Ariz.; 6, Sequoia N. P., Calif.; 7, Yosemite N. P., Calif.; 8, Crater Lake N. P., Ore.; 9, Mt. Hood N. F., Ore.; 10, Mt. Rainier N. P., Wash.; 11, Glacier N. P., Mont.; 12, Blackfeet Indian Reservation, Mont.; 13, Yellowstone N. P., Wyo.; 14, Teton N. F., Wyo.; 15, Grand Teton N. P., Wyo.; 16, Medicine Bow N. F., Wyo. (Haydn Division); 17, Medicine Bow N. F., Wyo.; 18, Black Hills N. F. and Harney N. F., S. D.; 19, Gunnison N. F., Colo. (See text for details.)

the brooms were conspicuous objects. All of the brooms were of the compact regular type, most of them being 2'-3' in diameter but occasionally slightly larger. Galls were especially prominent on the infected branches. The pycnia were clearly evident being very numerous at the tip of the leaf where they

appeared to be mature, becoming progressively fewer and less mature toward the base. They were also less abundant on the inner surface of the leaf, that is, the side adjacent to the branch.

CRATER LAKE NATIONAL PARK, OREGON

Infections of *Melampsorella* are not common in this park, although two collections by Weir have been made, according to specimens in the Forest Pathology Herbarium at Washington. A single witches' broom was located on *Abies magnifica* var. shastensis about 2 miles from the Park Headquarters on the road to the south entrance. It was growing on a lateral branch 2' from the trunk and 15' from the ground, reaching a size $5' \times 2' \times 3'$ but being very irregular. Most of the infected branches were $1\frac{1}{2}''-2''$ in length and the individual leaves were $1\frac{1}{2}''-1\frac{1}{2}''$ long, pale yellow in color, and bearing bright yellow conspicuous pycnia, which were scattered over the leaf, except in the stomatal areas. This witches' broom was very conspicuous with its pale yellow leaves and light colored branches against the dark green normal foliage. Conditions here are apparently unfavorable for the development and spread of this rust.

MOUNT HOOD NATIONAL FOREST, OREGON

The only observations and collections made in this area were taken on the road to Timberline Lodge at an elevation of about 5,000'. Most of the brooms were inaccessible but one collection was made. This specimen was from a small irregular witches' broom on a lateral branch bearing a prominent gall with several straggling hanging infected branches 1'-2' long. The host is Abies amabilis and represents what is believed to be a new locality for the disease on this host, it having been reported previously only in Washington. The disease is apparently not widely spread in this forest.

MOUNT RAINIER NATIONAL PARK, WASHINGTON

The situation here is similar in one respect to those mentioned in the last four areas, namely that there appear to be few infections. In the one area in Mt. Rainier National Park where the disease was collected the species on *Picea* was present. In this

respect it differed greatly from other areas along the coast where the rust occurred only on Abies. A total of 3 witches' brooms was observed, all on P. Engelmanni on the trail to Emmons Glacier, about 4/5ths of a mile from White River Camp Ground. Abies trees were also present in the immediate vicinity but were free from infection. By this time (see Table I) the aecia were beginning to mature and the broom was beginning to assume a yellowish-red tinge. The witches' brooms were typical of those found on Picea, being large and very irregular.

GLACIER NATIONAL PARK, MONTANA

In this area infections were found on both Picea Engelmanni and Abies lasiocarpa, the former being heavily attacked while on the latter brooms were found only occasionally. Along the Going-to-the-Sun Highway witches' brooms are especially conspicuous, some of them becoming very large and often occurring in considerable numbers. An interesting collection was made near Logan Pass on the stunted timberline growth of A. lasiocarpa. Under such adverse conditions the trees make but a small amount of annual growth, which would mean that it would be especially difficult for a rust to establish itself here. The trees were all about 9' tall and the witches' broom was $8'' \times 12''$ with very dense, compact growth. As might be expected the short growing season also affects the size of the brooms and the annual growth increment is very slight. The infected season's branches ranged from 1/4"-1" in length, the majority being between 1/4" and 1/2". That this represents the average annual growth is shown by studying the older branches of the broom. One branch 41/2" long was 9 years old. The growth each year, beginning with the current season, measured 1/2", 1/2", 1/2", 5/8", 5/8", 1/2", 1/2", 1/4", 1/4" respectively.

About 10 miles south of Glacier National Park in the Blackfeet Indian Reservation one collection was made on *Picea glauca*, which appears to be a new record for the rust on this host.

YELLOWSTONE NATIONAL PARK, WYOMING

Melampsorella is widely distributed on both Picea Engelmanni and Abies lasiocarpa throughout this entire area, the infections

varying from light to extremely heavy, in one case reaching epidemic proportions (Table II). In some areas the species on Abies was dominant, in other areas the situation is completely reversed. In no area were the two species ever found in a condition approaching equality. The results of the work in this area are summarized in figure 2. It will be noticed that the species on A. lasiocarpa was dominant in the region north of Canyon Junction around Mt. Washburn, where infections were heavy, and in the vicinity of Old Faithful, where the brooms were scattered. On the other hand the species on P. Engelmanni occurred rather widely throughout the Park (FIG. 2: Tables I and II) being in abundance in the region of Madison Junction and in epidemic proportions in one locality midway between Lake and Thumb, on Yellowstone Lake. In this latter area witches' brooms were found in practically every tree in the area; 95 brooms were found in 19 trees, 34 on one tree, 26 on another. Because the disease is so abundant and widely spread it provides an excellent opportunity for working out the distribution of two species and reference to figure 2 will indicate the two distinct distribution patterns.

Many very young infections were found, several consisting of single unbranched stems 1"-2" long growing on branches which were presumably free from the rust since they bore normal leaves. These cases were believed to represent very early infection, possibly occurring in the spring, although it is conceivable that infection may have taken place at some time during the preceding year, making these infections two years old. Irrespective of the time of infection, concerning which little or nothing is known, the invaded area was confined to the season's growth and the leaves were yellowish green in color and the stems slightly hypertrophied and pale brown in color. Most of these cases occurred on *P. Engelmanni*.

Two and three year old infections are characterized by the presence of supernumerary branches; one broom 3 years old had 2 main branches bearing a total of 22 infected branches, 10 being on one branch and 12 on the other. A young tree of *P. Engelmanni*, 12' in height, had 9 small witches' brooms, the largest being 6" in diameter, the remainder being much smaller and the

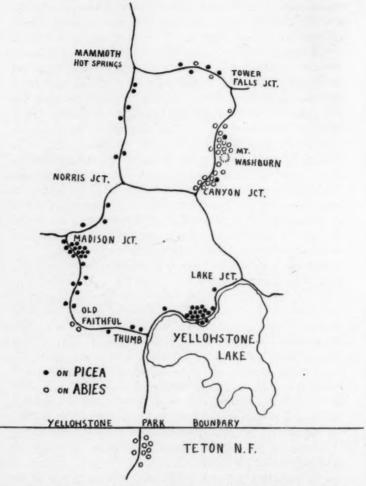


FIG. 2. Distribution patterns of infections in Yellowstone National Park, Wyoming. The disease is widely distributed throughout the area and two distinct patterns are evident. Solid circles represent infections on *Picea*, hollow circles represent infections on *Abies*. (See text for details.)

youngest being a single infected branch. One four year old infection was found on A. lasiocarpa with 10 infected branches, each being $1''-2\frac{1}{2}''$ in length, hypertrophied, pale in color, and bearing only the season's needles.

The rust was found on *Cerastium*, the alternate host, in great abundance in the Mt. Washburn area just below timberline within a few yards of a large specimen of *A. lasiocarpa* bearing several brooms. It would seem that conditions in this area are ideal from the standpoint of the spread of the disease. Both hosts are present in considerable numbers, there is an abundance of inoculum and conditions are favorable for the growth of the hosts as well as for infection. The problem of eradicating the disease from this area would be extremely difficult since the rust is systemic and perennial on *Cerastium* as well as on its coniferous hosts.

GRAND TETON NATIONAL PARK AND VICINITY

In the Teton National Forest extending southward from the southern boundary of the National Park numerous infections were found on A. lasiocarpa, particularly along the highway. In the Grand Teton National Park a few scattered infections were found on the same host along the east shore of Jenny Lake. One of these was a conspicuous broom being terminal on a lateral branch, about 4' from the ground and 3' from the trunk, very dense, compact, measuring $3' \times 2' \times 2'$, yellow in color and sporulating. The contrast between the diseased branch and the green foliage of the normal branches was striking. In the Hoback Canyon of the Wyoming National Forest Melampsorella was found on both hosts, moderately heavy on Picea and rather light on Abies. This area was not very thoroughly investigated and the situation in the small area examined in the Hoback Canyon may not be typical for the entire Wyoming National Forest.

The interesting feature of infections in this general area is the prevalence of the species on *Abies* in the Teton area while immediately north in Yellowstone National Park and south in the Wyoming National Forest the form on *Picea* was dominant.

MEDICINE BOW NATIONAL FOREST, WYOMING

This region proved to be very favorable for collecting and study due to the presence of the fungus and the respective hosts in quantity, and as a result this forest was studied rather intensively. The map (FIG. 3) and also the data in Tables I and II

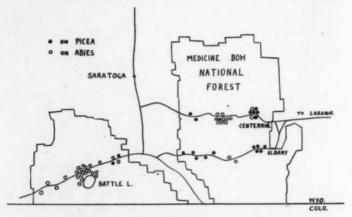


Fig. 3. Distribution of *Melampsorella* in the Medicine Bow National Forest, Wyoming. (See text for details.)

summarize the results obtained and demonstrate clearly the distribution patterns of these two species. In certain regions one species was definitely dominant while in other regions, often adjacent, the other species was abundant. For example, in the region of the University of Wyoming Summer Camp infections were heavy on *Picea*, scattered on *Abies*, yet in Libby Flats, a few miles west, the situation was completely reversed. West from Albany the *Picea* species was generally found in abundance.

In the western division of Medicine Bow National Forest, in the so-called Hayden Forest, infections were generally heavy on A. lasiocarpa, although a few were found on Picea between Encampment and the top of the Divide. In the region surrounding Battle Lake, an area was located where the species on A. lasiocarpa was in such abundance that it approached epidemic proportions. Witches' brooms occurred here in all sizes and in great numbers, each tree bearing one or more; one tree had 11 witches'

brooms all living and large, the largest being $2\frac{1}{2}' \times 2' \times 2'$. A young tree, 4' in height, had 8 witches' brooms on it, all young, 4 of them being year old infections. Many witches' brooms were on the main trunk; one broom $3' \times 2' \times 2'$ was located 3' from the ground almost completely girdling it. A few of the brooms reached a diameter of 4'-5', somewhat greater than the usual run of the brooms on Abies, due possibly to 2 or more infections becoming confluent. Aecia were beginning to mature but had not yet broken open; however, the young sori gave the brooms a distinctly yellow cast. A. concolor and P. Engelmanni occurred in this region but they were free from the disease.

BLACK HILLS AND HARNEY NATIONAL FOREST, S. D.

Melampsorella was found on the Black Hills Spruce P. glauca var. albertiana in the Black Hills N.F. in the vicinity of the Black Fox and Deerfield Camp Grounds, and in the Harney N.F. along the Highway north of Custer. In these regions infections were numerous, sometimes several occurring on one tree and ranging in size from 2'-4' in diameter. The brooms had a distinctly reddish cast due to the aecia which were mature. The genus Abies is not represented in this area.

GUNNISON NATIONAL FOREST, COLORADO

Although this evidence was collected during the summers of 1939 and 1940 it is being added here because it shows striking differences in the distribution of the two species. In the region of Gothic the species on *Picea* is definitely dominant, the brooms on *P. Engelmanni* being large, conspicuous and numerous, often in great masses in the tops of the trees. While *Abies* occurs throughout the region infections on this host were rare; in two years a total of only 6 witches' brooms were found on *A. lasio-carpa*. For further details on the disease in this area and for photographs of typical infections reference should be made to a recent paper (6).

DISCUSSION

From the taxonomic standpoint distribution is sometimes important in the delineation of species. The obligate parasites

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being completely dependent upon their hosts are thus limited in their distribution by the range of their hosts. Melampsorella, like other rusts, has developed a high degree of specialization on a specific group of plants particularly in the gametophytic phase on the coniferous hosts which has led to the formation of two distinct species. The two aecial hosts, Picea and Abies, being much alike in their ecological relationships, are very similar in their distribution, as for example, P. Engelmanni and A. lasiocarpa. It would be expected, therefore, that the two rusts would be very similar in their general distribution. However, it might be supposed since they have each developed through the centuries their own morphology, that differences might also exist in their physiology. This would be evident in the time of infection, conditions required for establishment of the infection, and for the continued growth of such infections, so that in a given area conditions might be more favorable for the development of one species, while in another area they might be more favorable for the development of the other. Such seems to be the case in Melampsorella. In every heavily infected area visited, one or the other species was found to be dominant, while in areas lightly infected it was often difficult to be sure which species was the more abundant, since only a small number could be examined. In a few cases such as in the Black Hills and in California only one of the two coniferous hosts was present, and therefore the evidence here would be of less significance.

In the forests of California, Oregon, Washington, the disease is not severe and occurs usually as isolated scattered infections, whereas in the Rocky Mountain States it is widely spread, abundant and in certain areas (Table II) of epidemic proportions. In these latter areas witches' brooms are found on all sizes of trees and in all stages of growth. One tree for example, 4' in height, had 2 witches' brooms, one of which completely surrounded the trunk and extended to within 6" of the tip. Other young trees have been found with 7–8 brooms upon them. The demands of such infections become very great when it is realized that each year the number of new infected branches is sharply increased, particularly when the broom has reached a diameter of one or more feet. The tree is thus handicapped in its struggle

for existence, and its growing period is probably greatly short-ened. If the infection involves the terminal growing point, the tree becomes stunted and often dies prematurely. The probable effect of a large witches' broom girdling the main trunk would be to interfere greatly with normal translocation. It is a common sight to see a large tree, particularly of *Picea*, with a great mass of branches surrounding the trunk and the tree dead above the infections. On the basis of many observations on all sizes of trees infected in varying degrees, it would appear that light infections cause a relatively insignificant amount of damage, moderate infections result in some injury especially to young trees which may be prematurely killed, while heavy infections are always serious on both old and young trees, shortening the growing period of the former and usually killing the latter.

Another effect of a main trunk infection appears to be the gradual weakening of the tree at that point. In the Grand Canyon National Park many old trees were observed which had been snapped off at a point marked by several old witches' brooms, suggesting that the rust mycelium had gradually weakened the trunk at that point making it susceptible to breakage. In the opinion of the writer this disease is sometimes more serious than has been generally recognized.

A few cases of growing point escapes were observed similar to those reported in a previous paper (6). The growing point usually of a lateral branch, after being infected, outgrows the infection leaving the mycelium in a definite area on the branch, from which by supernumerary secondary buds, small brooms are formed at the nodes. It is not known whether the mycelium is capable of invading healthy tissue of the older part of the branch, but it seems doubtful. On most brooms the mycelium invades only the season's growth, since it is systemic in the meristematic regions. Only one broom was found which contained a mixture of healthy and diseased branches. The broom was large and conspicuous but was greenish in color due to the large number of healthy leaves. Many of the branches appeared to be perfectly healthy but when examined closely were found to have one or two small infected leaves. Some of the branches were lacking in leaves, indicating infection, but the season's branches were normal; in one case involving 3 new shoots arising from one branch, 2 were infected and the other was free. On this same branch at another place all of the leaves were infected except one leaf at the base of the branch. On another branch which appeared healthy, that is the needles had been retained for the last 5 years, 5 or 6 of the leaves were found to bear pycnia. This was the only broom found where all of the buds were not systemically infected. In this case the fungus had failed to become established, and the host may be simply outgrowing the fungus. The condition was evidently a local one since the same tree bore two other brooms which were typical in every respect.

Apical dominance appears to be present in the brooms on *Picea*, the terminal branch often growing 6''-8'' during the season while the supernumerary lateral branches are much shorter, thus giving rise to a diffuse type of broom, with many prominent irregular branches, which sometimes reach a diameter of 4'-6' or become even larger. In the form on *Abies* apical dominance is apparently lacking and the lateral buds, which seem to be more numerous, make almost as much growth as the terminal bud, resulting in a very compact type of broom with a great many relatively uniform branches, rarely exceeding a diameter of 2'-3'. These differences found so consistently indicate clearly that these two types of witches' brooms are due to a fundamentally different manner of growth.

Geotropic disturbances are evident in both types of infection. Normally, lateral branches are transversely geotropic while the terminal bud of the main trunk is negatively geotropic. It has been noted many times on both *Picea* and *Abies* that the infected branches become at once negatively geotropic. In one case on a lateral branch of *A. lasiocarpa* in the Uintah National Forest the infection stood out sharply at right angles to the branch projecting upwards about 8". An interesting specimen was collected on *P. Engelmanni* in the Medicine Bow National Forest. The infection was about 1½ high, very regular and compact. It appeared to be growing directly on the ground but when examined closely was found to be at the end of a long lateral branch. This branch originated at the base of a tree about 6' distant and was completely covered with leaves and debris.

This was a very conspicuous example of altered tropism since the broom was growing at an almost perfect right angle to the lateral branch.

Conclusive proof of the existence of two species would be furnished by inoculations to the alternate hosts Cerastium and Stellaria and then inoculations back to the aecial hosts. During the summer of 1941 infection studies were commenced and are being continued, the results of which will be published later. At the present time it is not known if differences also exist in the uredo and telial stages of these two species, nor is it known exactly when infection to Abies and Picea takes place. The fact that the diploid sporophytic mycelium on Cerastium is also systemic and perennial increases greatly the opportunities for successful infections. An attempt is being made to work out the species of Cerastium and Stellaria which harbor the alternate stage and to obtain comparative material. Preliminary experiments seem to indicate that the same species of Cerastium harbor both species of Melampsorella, which confirms Weir and Hubert's observation (8) although Arthur (1) considers this to be improbable due to the unlike nature of the pycnia. The situation is comparable to that of Cronartium coleosporioides where the aecia assume "three fairly distinguishable forms which have been shown by culture to produce uredia and telia of identical appearance on the same species of Castilleja" (2). The three forms were treated first by Arthur as distinct species, later as varieties (2). The very great differences in the morphology and physiology of the haploid stages of Melampsorella constitute adequate evidence for the establishment of two species even if the diploid stages should prove to be identical.

SUMMARY

Further evidence for the existence of two species of *Melampso-rella* was obtained from a study of their distribution. Many areas in the Western States were visited during the summer of 1941, and in the forests where both hosts and the disease were found detailed studies were made on the distribution of the two forms. Seventy-five collections and over 150 detailed observations were made. In practically every area visited one or the

other species was found to be dominant, even though both hosts were abundant, indicating that these two species differ in their physiology as well as in their morphology. Two distinct distribution patterns were thus obtained.

The disease was collected in the following National Forests: Uintah N.F., Wasatch N.F., Powell N.F., Utah; Kaibab N.F., Ariz.; Mt. Hood N.F., Ore.; Teton N.F., Wyoming N.F., Medicine Bow N.F., Wyo.; Harney N.F., Black Hills N.F., S. D.; and in the following National Parks: Grand Canyon N.P., Ariz.; Sequoia N.P., Yosemite N.P., Calif.; Crater Lake N.P., Ore.; Mt. Rainier N.P., Wash.; Glacier N.P., Mont.; Yellowstone N.P. and Grand Teton N.P., Wyo.

In the forests of the Rocky Mountain States where *Picea* and *Abies* are abundant the disease was found to be more severe than heretofore believed. Many trees were found to be partially or completely dead; many were dwarfed or stunted. In some areas in Wyoming the disease occurred in such abundance that it was considered to be of epidemic proportions.

Trunk infections were found to be particularly harmful. In the Grand Canyon National Park many older trees were found which had been broken off evidently due to weakening of the main trunk at that point. Trunk infections of young trees soon cause their death.

Differences in growth habits which produce a dense, compact broom on *Abies* and an irregular diffuse broom on *Picea* were found to be a constant and fairly reliable character, and are believed to be due to apical dominance which is present in the species on *Picea* and absent in the species on *Abies*.

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A TAXONOMIC STUDY OF THE GENUS HANSENULA¹

C. L. BEDFORD 2

Since yeasts are of importance in several unrelated fields of investigation a great deal of confusion has arisen in their classification. While the classification systems of Stelling-Dekker (1931) for ascospore-forming yeasts and of Lodder (1932, 1934) for anascosporogenous yeasts have gained almost complete universal acceptance and are a vast improvement over the confusion which preceded them, they are still incomplete and difficult to use. The placing of a given strain in a particular genus is not easy and even more difficulty is experienced in differentiating between the species belonging to a given genus.

The purpose of this investigation has been to obtain more definite information concerning the morphology and taxonomy of the closely related species of the genus *Hansenula*.

EXPERIMENTAL PROCEDURE

In this investigation a study was made of 100 cultures of yeast obtained as species of *Hansenula* from various sources in the United States, Europe, Asia and South Africa with 14 species of *Hansenula* represented. These cultures were obtained from the collection of yeasts of the Fruit Products Laboratory, University of California, Berkeley, and are listed in Table I.

The morphological characteristics were determined essentially by the methods described by Stelling-Dekker (1931). Cell size was determined on cultures grown in 15° Balling unhopped beer wort and in synthetic medium (0.1 per cent KH₂PO₄, 0.1 per cent (NH₄)₂SO₄, 0.05 per cent MgSO₄ and 5 per cent glucose). Observations were also made on cultures grown in 15° Balling wort agar and wort gelatin. For spore formation carrot, beet and

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¹ This paper is part of a thesis submitted in partial satisfaction of requirements for the degree of Doctor of Philosophy, University of California.

potato wedges, Gorodkowa agar and gypsum blocks were used. For those cultures that did not sporulate on these media, other media as grape, prune and cherry juice and agar, liquid wort and wort agar, synthetic medium with 10 per cent glucose, lactose and sucrose alone and with the acids tartaric, citric and malic in concentrations of 0.1 per cent were tried. The method of Stantial (1928, 1935) was also used.³ All sporulation tests were stored

TABLE I

	0.1.0.1.1	Source				
Number	Culture Studied	Person	Country	Writer's Identification		
1			India	H. saturnus		
3 5	Grapes	Mrak	California			
3	Grapes	Mrak	California	H. anomala		
. 5	H. saturnus	A.T.C.C.4		H. saturnus		
6	H. anomala	A.T.C.C.	1	H. anomala		
7	H. anomala *	Takahashi	Japan	H. anomala		
8	Concentrated sugar- egg mixture	Baker	California	H. subpelliculosa		
9	44	Baker	California	H. subpelliculosa		
10	46	Baker	California	H. subpelliculosa		
11		Baker	California	H. subpelliculosa		
13	H. Schneggii	C.B.S.s	Holland	H. Schneggii		
14	H. anomala var. sphaerica	C.B.S.	Holland	H. anomala		
17	Bottled white wine	Funch	California	H. anomala		
19	Simple sirup 31° Be.	Mrak	California	H. anomala var. sphaerica		
20	Simple sirup 31° Be.	Mrak	California	H. anomala		
21	Simple sirup 31° Be.	Mrak	California	H. anomala		
22	Simple sirup 31° Be.	Mrak	California	Brettanomyces bruxellansis		
23	Simple sirup 31° Be.	Mrak	California	H. anomala		
24	Simple sirup 31° Be.	Mrak	California	H. anomala		
25	Simple sirup 31° Be.	Mrak	California	H. anomala var. sphaerica		
26	Sugar sirup	Mrak	California	H. anomala		
27	Soil	Cruess	California			
28	Grapes	Mrak	California	Candida Krusei		
29	011	Mrak	California	H. anomala var. sphaerica		
30	Olives	Vaughn	California	Pichia fermentans		
31	Soil	Mrak	California	H. anomala var. sphaerica		
32	Sweet wine	Mrak	California	H. anomala		
33	Apricot extract	Mrak	California	H. anomala var. sphaerica		
34	Grapes	Mrak	California	H. anomala var. sphaerica		
36	Grape juice	Mrak	California	TI		
37	Willia sp. No. 83	Kroemer and Krumboholz	Holland	H. anomala var. sphaerica		
38	H. anomala		Germany	H. anomala		
39	H. anomala I		Germany	H. anomala		
40	H. anomala II		Germany	Pichia fermentans var. rugoso		
41	H. saturnus	-	Germany	H. anomala var. sphaerica		
42	H. panis	Castelli	Italy	H. anomala		
43	Dried prunes	Mrak	California	H. anomala		
45	Dried prunes	Mrak	California	H. anomala var. sphaerica		
46	Dried prunes	Mrak	California	Candida Krusei		
47	Dried prunes	Mrak	California	H. anomala var. sphaerica		
48	Dried figs	Mrak	California	H. anomala var. sphaerica		
49	Dried pears	Mrak	California	H. anomala var. sphaerica		
50	Dried apricots	Mrak	California	H. anomala var. sphaerica		
51	Dried prunes	Mrak	California	H. anomala var. sphaerica		
52	Sugared dried prunes	Mrak	California	H. anomala		
53	Dried prunes	Esau No. 190	California	Pichia fermentans		
54	Prune debris	Mrak	California	Pichia fermentans		
55	Dehydrated prunes	Mrak	California	H. subpelliculosa		

³ This study was made by B. L. Smith.

⁴ A.T.C.C. American Type Culture Collection, Washington, D. C.

⁸ C.B.S. Centraalbureau voor Schimmelkulturs, Bairn, Holland.

TABLE I-Continued

Number	Culture Studied	Source		William In Value I Constitution	
Number	Culture Studied	Person	Country	Writer's Identification	
56	Dried prunes	Mrak	California	H. subpelliculosa	
57	Dried prunes	Mrak	California	H. subpelliculosa	
58	Dried prunes	Mrak	California	H. subpelliculosa	
59	Dried prunes	Mrak	California	H. subpelliculosa	
60	Dried prunes	Mrak	California	H. subpelliculosa	
61	Dried prunes	Mrak	California	H. subpelliculosa	
62	Dried prunes	Mrak	California	H. anomala var. sphaerica	
63	Dried prunes	Mrak	California	H. anomala	
64	Dried prunes	Mrak	California	H. anomala	
65	Dried prunes	Mrak	California	H. subpelliculosa	
66	Sugared dried prunes	Mrak	California	H. anomala var. sphaerica	
67	Sugared dried figs	Mrak	California	H. anomala	
68	H. saturnus		Poland	H. saturnus	
69	H. anomala		Poland	Pichia chodati	
70	H. saturnus	Winge No. 64	Holland	H. saturnus	
71	Arnold sirup	Mrak	California	H. anomala var. sphaerica	
72	Arnold sirup	Mrak	California	Candida Guilliermondi	
73	Arnold sirup	Mrak	California	Torulopsis sp.	
7.5	H. nivea	Castelli	Italy	H. anomala	
76	Arnold sirup	Mrak	California	Zygohansenula californica	
77	Fountain sirup	Mrak	California	Torulopsis ap.	
78	H. Ciferri	Lodder	Holland	H. Ciferri	
79	Arnold sirup	Mrak	California	H. anomala	
81	Arnold sirup	Mrak	California	H. anomala var. sphaerica	
82	Arnold sirup	Mrak	California	Candida Guilliermondi	
84	H. anomala var.	C.B.S.	Holland	H. anomala var. sphaerica	
85	H. anomala var. sphaerica	C.B.S.	Holland	H. anomala var. heteromorphe	
86	H. anomala	Winge No. 119	Holland	H. anomala var. sphaerica	
87	Hansenula sp.	Winge No. 94	Holland	H. anomala var. longa	
88	H. anomala var. longa	C.B.S.	Holland	H. anomala var. longa	
89	H. anomala var.	C.B.S.	Holland	H. anomala var. longa	
90	H. javanica	C.B.S.	Holland	H. anomala var. sphaerica	
91	H. anomala var. robusta	C.B.S.	Holland	H. anomala var. longa	
92	H. panis	C.B.S.	Holland	H. anomala var. longa	
93	H. saturnus	C.B.S.	Holland	H. saturnus	
94	H. lambica	C.B.S. C.B.S.	Holland	H. lambica	
95 96	H. nivea Zygohansenula cali- fornica	Lodder	Holland Holland	H. anomala var. longa Zygohansenula californica	
97	H. suareolens	C.B.S.	Holland	H. suaveolens	
98	Olives	Vaughn	California	Candida Krusei	
99	Olives	Vaughn	California	Candida Krusei	
101	Olives	Vaughn	California	Candida Krusei	
102	Olives	Vaughn	California	Candida Krusei	
103	Olives	Vaughn	California	Pickia Kluyveri	
104	Hansenula sp.	Niehaus	Africa	H. anomala	
105	H. javanica	C.B.S.	Holland	H. anomala var. longa	
106	H. anomala	C.B.S.	Holland	H. anomala var. heteromorphe	
107	Olive brine 58° S.	Douglas	California	H. anomala var. sphaerica	
108	Olive brine 28° S.	Douglas	California	H. anomala var. sphaerica	
109 110	Green olive tank Fresh water olive tank	Douglas Douglas	California California	H. anomala var. sphaerica H. anomala	

at a temperature of 20–25° C. for more than six weeks if necessary. Colors were reported according to the nomenclature of Ridgway (1912) and cultural characteristics according to the customary terminology used by bacteriologists, e.g. Levine (1933). Pseudomycelium formation was determined by the method of Rivalier and Seydel (1932) using their medium and wort agar. Fermentation tests were made using the Durham (1898) tube

technique. The yeast juice medium described by Stelling-Dekker (1931) was used in the fermentation tests. The quantitative method of van Iterson-Kluyver (see Stelling-Dekker) was used when doubtful results were obtained and to determine the amount of raffinose fermented.

The ability of the organisms to utilize the various carbon and nitrogen compounds was determined by growth of the organisms and utilization of the compounds in a liquid synthetic medium. (NH₄)₂SO₄ and glucose were replaced by the compounds to be studied. The nitrogen compounds were added in concentrations sufficiently low (5 mg. N per 100 ml.) so that the amount as well as the utilization could be determined quantitatively.

The production of esters was determined qualitatively and quantitatively using grape juice and synthetic medium with glucose and ethyl alcohol. Yeast juice plus glucose was also used but ester production was only determined qualitatively.

SYSTEMATIC TREATMENT

A number of investigators have contributed to the study of the taxonomy and morphology of the genus *Hansenula*. The generic characters of the genus *Hansenula* Sydow have been defined by Hansen (1904), Guilliermond (1928, 1936) and Stelling-Dekker (1931).

Hansen (1904) characterized the genus as yeasts forming a film on sugar nutrient media. Spores hat or lemon shaped, smooth-walled with one membrane and a very prominent ledge. Most species form esters; a few do not ferment. Germination of spores by budding.

Stelling-Dekker (1931) defined the genus as follows: Cells of various shapes, round, oval or elongated; vegetative reproduction by many-sided budding, often clusters of buds. A pellicle, dry on account of the co-mixture of air, and dull, formed at once in sugar nutrient media. Spores hat-shaped, oblate, globular or Saturn-shaped. Vigorous fermentation. Nitrate assimilation positive; with ethyl alcohol a vigorous growth with formation of a membrane. Esculin cleavage positive.

Guilliermond (1936) recently described the genus as yeasts with oval or elongated, rarely round cells, occasionally rudiments

of mycelium. Asci formed with conjugation; 1–4 ascospores having the aspect of hats or surrounded by a projecting collar. In certain forms (*H. saturnus*) conjugation between ascospores or more generally between the first cells issued by their budding yields zygospores, initial point of numerous generations of diploid cells transformed then to asci. Fungi develop initially in liquid medium as a pellicle. Oxidation and occasionally fermentation.

On the basis of this investigation the genus has been redefined as follows: Cells of various shapes, spherical, oval or elongated. Vegetative reproduction by many-sided budding. Pellicle formed on liquid medium, well-developed or very slight. Conjugation may or may not immediately precede ascospore formation. Spores hat- or Saturn-shaped. Vigorous fermentation. Nitrate and nitrite assimilation positive (auxanogram method of Beijerinck). Growth with ethyl alcohol. Esculin and salicin hydrolyzed.

The genus is divided into two subgenera, namely Hansenula and Zygohansenula following Klocker's (1924) procedure for the genus Pichia. This is also in agreement with the view expressed by Lodder (1932).

The definition of the subgenus *Hansenula* is as for the genus *Hansenula* with the added characteristic that no conjugation immediately precedes ascospore formation.

The definition of the subgenus Zygohansenula is as for the genus Hansenula with the added characteristic that conjugation immediately precedes ascospore formation.

In 1931 Stelling-Dekker carefully studied the species of Hansenula described by the various authors and accepted, as valid species or varieties, the following, which also includes those recently described by Lodder (1932) and Castelli (1937). H. saturnus (Klocker) Sydow, H. anomala (Hansen) Sydow, H. anomala var. sphaerica (Naegeli) Dekker, H. anomala var. productiva Dekker, H. anomala var. longa Dekker, H. anomala var. robusta Dekker, H. javanica (Groenewege) Dekker, H. Schneggii (Weber) Dekker, H. Ciferri Lodder, H. suaveolens (Klocker) Dekker, H. panis Castelli, H. nivea Castelli and Zygohansenula californica Lodder. Two species, H. Wichmanni described by

Zikes (1906) and *H. fermentans* described by Verona and Vallegg! (1933), are not available as they have been lost. Since Stelling-Dekker's treatment of the genus *Hansenula* is more complete than any other systematic treatment of the genus it is the logical system to follow. At the present time several species and varieties are separated by minor characters and it is very difficult to distinguish these species and varieties with certainty. Thus in this investigation an attempt has been made through a more complete morphological study to obtain criteria whereby the species or varieties can be identified more easily.

The cultures studied showed considerable similarity in morphological characteristics with the exception of cell size. The slant cultures, giant colonies, films, spore formation, and pseudomycelia are all very similar and as a whole give no sound basis for the separation of the various varieties. Therefore, with the exception of a few cultures, cell size, as used by Stelling-Dekker (1931), appears to be the only possible means at the present time for the separation of varieties or species. This is not entirely satisfactory as when different media are used for growth and measurement of the cells considerable variations are obtained.

In his fundamental researches Hansen used hopped wort whereas other research workers have undoubtedly used unhopped wort, although records are frequently lacking. This is of fundamental importance as the presence or absence of hop extract in the medium will influence the shape and size of the individual cells. The manner in which the wort is made will also have an influence on the shape and size of the cells. It should be noted that Stelling-Dekker in her excellent work described exactly the method used for making unhopped wort.

The examination of the cultures in this study showed some variation in cell size in different lots of liquid wort and therefore liquid synthetic medium was used to determine whether this variation could be eliminated. The shape and size of the cells in synthetic medium, in some cases, varied considerably from those formed in liquid wort, e.g. a number of cultures that form elongate cells in liquid wort form only spherical and oval cells in synthetic medium. However, the results obtained were more

consistent and it seems that the use of a synthetic medium for the measurement of cells would be more suitable for this genus than liquid wort as its use would eliminate the variations that occur in natural media, such as liquid wort, due to the different methods of preparation and variations in material used for its preparation and would facilitate the comparing of results obtained by various investigators as pure chemicals are available to all for its preparation.

The physiological studies show, as a whole, very little difference between the species of *Hansenula* with the exception of their fermentative powers. The cultures have therefore been grouped for taxonomic treatment on the basis of cell size in synthetic medium and fermentative characteristics in most cases.

HANSENULA ANOMALA (Hansen) Sydow.

Syn: H. anomala var. sphaerica (Naegeli) Dekker (14), H. panis Castelli (42) and H. nivea Castelli (75).

Twenty-three cultures were placed in this species.

Cells spherical, oval and elongate in 3 and 10 day liquid synthetic medium. Dimensions of cells from film on synthetic medium $1.75-6 \times 2.35-19 \mu$ at 3 days and $1.75-8 \times 2.35-19 \mu$ at 10 days. Spores hat-shaped, $1.75-2.35 \times 2.35-3 \mu$, 1-4 per ascus. Films form on liquid medium within 48 hours; on synthetic medium smooth to slightly rugose, tending to become farinose; on liquid wort smooth to rugose. Sediment increases with time. 60 day wort gelatin giant colonies smooth to farinose, occasionally actinomorphic stripes in the colony, flat to umbonate, edges entire to undulate, dull, buff to white. 60 day wort agar slants, smooth to vesicular, slopes smooth to slightly contoured, raised to convex, edges entire to lobate-lobulate, periphery plumose, dull to glistening, light buff. 30 day synthetic agar slants, slightly rugose to rugose, convex, edges lobatelobulate, dull, light ivory. Pseudomycelia of elongate cells on wort agar with spherical and oval blastospores. Ferments glucose, fructose, mannose, sucrose, maltose, galactose, and raffinose (1/3). Does not ferment arabinose, xylose, lactose, glycerol, mannitol or dextrin. Nitrate and nitrite assimilated, sarcosine not assimilated. Forms ester in grape juice, synthetic medium with glucose or ethyl alcohol, yeast juice with glucose. Ethyl alcohol utilized. Esculin and salicin hydrolyzed.

Cultures 26 and 29 do not utilize guanidine as a nitrogen source and 39 does not ferment galactose. However these differences are not sufficient to justify the separation of these cultures as varieties or types.

HANSENULA ANOMALA var. SPHAERICA (Naegeli) Dekker.

Syn: H. anomala (Hansen) Sydow (86) and H. javanica (Groenewege) Dekker (90).

Twenty-four cultures were placed in this variety.

This variety is similar to *H. anomala* except cells on liquid synthetic medium, spherical to oval, occasionally somewhat elongate. Dimensions of cells from films, $1.75-7 \times 2.35-10 \,\mu$, few up to $12 \,\mu$.

In this group cultures 19, 33, 34, 41, 45, 47, 48, 49 and 86 do not utilize guanidine as a nitrogen source. Cultures 45, 48, and 50 do not assimilate α methyl glucoside. These, however, do not justify the establishment of new varieties.

HANSENULA ANOMALA var. LONGA Dekker.

Syn: H. anomala var. productiva Dekker (89), H. anomala var. robusta Dekker (91), H. panis Castelli (92), H. nivea Castelli (95) and H. javanica (Groenewege) Dekker (105).

Six cultures were placed in this variety.

Cells grown in liquid synthetic medium, spherical, oval to very elongate, chains of elongate cells at 3 and 10 days. Dimensions of cells from films at 3 and 10 days, $1.25-5 \times 2.35-30 \,\mu$. Films on liquid wort rugose to folded, on synthetic medium smooth to slightly rugose. 60 day wort gelatin giant colonies, smooth to farinose, flat to umbonate, edges entire to undulate, dull, buff to white. 60 day wort agar slants smooth to rugose or verrucose, flat to convex, slopes slightly vesicular to rugose, edges entire to lobate-lobulate, periphery plumose, dull, light buff. 30 day synthetic agar slants, rugose, convex, edges entire to lobate, light ivory. Other characteristics as H. anomala.

Culture 87 differs from the above in that the film on liquid wort is smooth with 1-4 folds at 3 and 10 days. 30 day synthetic agar slant light rose in color. This, however, is not sufficient to justify the establishment of a new variety.

Hansenula anomala var. heteromorpha var. nov.

Syn: H. anomala var. sphaerica (Naegeli) Dekker (86) and H. anomala (Hansen) Sydow (106).

This variety is similar to *H. anomala* var. *longa* except culture 106 forms pseudomycelia of heteromorphic cells in liquid synthetic medium at 3 and 10 days.

Cells spherical, oval, oblong, pyriform and slender elongate. Few free cells. Culture 85 at 3 days in liquid synthetic medium, cells spherical, oval to elongate, $2.35-4.7 \times 3.5-16.5 \,\mu$ at 10 days as 106 but with free cells.

The difference between the two cultures is the time necessary for the formation of pseudomycelia and this is not sufficient for their separation.

Hansenula subpelliculosa sp. nov.

Eleven cultures were placed in this species. These were isolated from concentrated sugar-egg mixture and dried prunes.

Cells spherical to oval at 1, 3, 10 days in liquid wort and in liquid synthetic medium at 3 and 10 days. Dimensions of cells $2.2-7 \times 2.2-9 \mu$, occasional large spherical cells 9.5–11 \times 9.5–11 μ . Spores hat-shaped, $1.75-2.35 \times 2.35-3 \mu$, 1-2, 3-4 per ascus. Films on liquid wort and synthetic medium very thin or none, ring formed in 10 days. Sediment increases with time. 60 day wort gelatin giant colonies flat to slightly umbonate, smooth to slightly contoured, border undulate, dull, buff. Culture 60 differs in being rugose. 60 day wort agar slants convex, flattened surface smooth to slightly vesicular or verrucose, slopes slightly contoured, border entire to lobate-lobulate, glistening, periphery plumose, light buff. 30 day synthetic agar slants smooth, glistening, light ivory. Pseudomycelia of elongate cells on wort agar with spherical and oval blastospores. Ferments glucose, fructose, mannose, maltose, sucrose and raffinose (1/3). Does not ferment galactose, lactose, xylose, arabinose, glycerol, mannitol or dextrin. Nitrate and nitrite assimilated (auxanogram method). Forms ester in grape juice and yeast juice with glucose. Growth in synthetic medium very slow and poor. Ethyl alcohol utilized. Esculin and salicin hydrolyzed.

Cultures 8, 9, 10, 11, 55 and 58 do not utilize galactose. Culture 61 differs in that 60 day wort gelatin giant colony rugose, alveolate, umbonate, border undulate, dull, buff and it does not

ferment maltose. These differences are not sufficient for the establishment of a new variety.

The lack of a good film on liquid wort and very poor growth in synthetic medium differentiates this species from the others and justifies the establishment of a new species.

HANSENULA SATURNUS (Klocker) Sydow.

Five cultures were placed in this species.

Cells spherical to oval at 1, 3 and 10 days in liquid wort and synthetic medium. Dimensions of cells from films on liquid wort $2.5-7 \times 3.5-8 \mu$ at 1 and 3 days, $3-8 \times 3.5-8 \mu$ at 10 days; on synthetic medium $2.35-8 \times 3-9 \mu$ at 3 and 10 days. Giant cells in 3 and 10 day synthetic medium 7-11 \times 8.5-12 μ . (sprossverbände) in synthetic medium at 3 and 10 days. Saturn-shaped, $1.75-3 \times 2.35-3 \mu$, 1-2 per ascus. Films on liquid wort and synthetic medium at 48 hours, rugose on wort and smooth on synthetic medium; becomes rugose on synthetic medium at 6 days. Sediment increases with time. 60 day wort gelatin giant colonies mostly smooth with irregular farinose and rugose surface markings, dull, buff with surface markings chalky white. 60 day wort agar slants convex, flattened surface slightly vesicular, slopes slightly contoured, borders lobate-lobulate, dull, light buff. 30 day synthetic agar slants convex, rugose, borders lobate-lobulate, dull, light ivory. Ferments glucose, fructose, mannose, sucrose, and raffinose (1/3). Does not ferment galactose, maltose, lactose, xylose, mannitol, glycerol or dextrin. Nitrate, nitrite and sarcosine assimilated, succinimide not assimilated. Does not utilize galactose, maltose, erythitol, a methyl glucoside, phloridzin and malonic acid. Forms a small amount of ester in grape juice, synthetic medium with glucose or ethyl alcohol, yeast juice with glucose. Ethyl alcohol utilized. Esculin and salicin hydrolyzed.

HANSENULA SUAVEOLENS (Klocker) Dekker (97).

Cells spherical to oval in liquid wort and synthetic medium at 1, 3, 10 and 3 and 10 days respectively. Dimensions of cells from films on liquid wort $2.5-5.25 \times 3.5-8~\mu$ at 1, 3 and 10 days; from films on synthetic medium $3.5-7 \times 3.5-7~\mu$. Clusters (sprossverbände) in synthetic medium at 10 days. No sporulation obtained. Films on liquid wort and synthetic medium within 24 hours, rugose on liquid wort and smooth on synthetic medium. Sediment increases with time. 60 day wort gelatin giant colonies, flat to slightly raised, smooth, dull, buff. 60 day

wort agar slants raised, center finely verrucose, borders lobate-lobulate, dull, periphery plumose, light buff. 30 day synthetic agar slants convex, slightly rugose, borders lobulate, dull, light ivory. Fermentation of glucose, fructose, mannose, sucrose and raffinose (1/3). Does not ferment galactose, maltose, lactose, xylose, arabinose, mannitol, glycerol or dextrin. Nitrate and nitrite assimilated, sarcosine and succinimide not assimilated. Does not utilize arabinose, erythitol, α methyl glucoside, phloridzin, citric or malonic acids. Forms little ester. Ethyl alcohol utilized. Esculin and salicin hydrolyzed.

Hansenula Ciferri Lodder (78).

Cells spherical to oval in liquid wort and synthetic medium. Dimensions of cells from films on liquid wort 3.5-8 x 3.5-8 u at 1, 3 and 10 days; from films on synthetic medium 2.35-6 X 2.35-6 µ at 3 and 10 days. Clusters (sprossverbände) in synthetic medium at 3 and 10 days. Spores hat-shaped, 1.75- $2.35 \times 2.35 - 3 \mu$, 2-4 per ascus. Films on liquid wort and synthetic medium as islets in 2 days, complete in 4 days, smooth, thin. 60 day wort gelatin giant colonies with depressed center, edge corrugated, border undulate, moist, glistening, buff. Gelatin slightly liquefied in center. 60 day wort agar slant raised, center vesicular, slopes smooth, borders lobulate, dull, periphery slightly plumose, light buff. 30 day synthetic agar slant convex, smooth, borders lobulate, dull, light ivory. Pseudomycelia of elongate cells on wort agar, blastospores spherical and oval. Fermentation of glucose, fructose, mannose, galactose, sucrose, maltose, and raffinose (1/3). Does not ferment lactose, xylose, arabinose, glycerol, mannitol or dextrin. Nitrate and nitrite assimilated, cysteine, succinimide or guanidine not assimilated. Does not utilize citric, malic, malonic, acetic, lactic or fumaric acids. Forms slight amount of ester. Ethyl alcohol utilized. Esculin and salicin hydrolyzed.

During the culturing of this species in liquid wort it lost its ability to sporulate and to form elongate cells. However, a later examination of a six month old agar slant showed the presence of elongate cells. When this was transferred to liquid wort spherical, oval and a few elongate cells were present in the film. In the suspension and sediment very elongate cells $(2.5-5 \times 10-29\,\mu)$ and pseudomycelia were found. On transferring this active culture to carrot wedges spores were observed in abundance after six days. Thus it appears that when successive

transfers are made in liquid wort the ability to form elongate cells is lost and also the ability to sporulate. The spores were formed in spherical and oval asci. Few elongate cells were present on carrot wedges.

HANSENULA SCHNEGGII (Weber) Dekker (13).

Cells spherical, oval to elongate in liquid wort and synthetic medium. Dimensions of cells from films on liquid wort 2.5- $3.5 \times 5.25 - 10.5 \,\mu$ at one day, $1.25 - 5 \times 5.25 - 14 \,\mu$ at 3 and 10 days: from films on synthetic medium $2.35-7.5 \times 4.5-14 \mu$ at 3 and 10 days. Pseudomycelia of elongate cells on wort agar, blastospores spherical and oval. No sporulation obtained. Film on liquid wort in 24 hours, rugose; on synthetic medium slightly rugose at 2 days, smooth at 6 and 12 days. Sediment increases with time. 60 day wort gelatin giant colonies flat, smooth, border undulate, dull, covered with farinose white layer. 60 day wort agar slant slightly convex, slightly rugose, border entire to slightly lobulate, dull, periphery plumose, chalky white. 30 day synthetic agar slant convex, slightly rugose, borders lobulate, dull, light ivory. Fermentation of glucose, fructose, mannose and maltose vigorous, sucrose slowly and galactose very slightly. Does not ferment rafflnose, xylose, arabinose, glycerol, mannitol or dextrin. Nitrate and nitrite assimilated, guanidine, sarcosine or succinimide not assimilated. Forms ester in grape juice, synthetic medium with glucose or ethyl alcohol, yeast juice with glucose. Ethyl alcohol utilized. Esculin and salicin hydrolyzed.

The characteristics of this species agree with those given by Stelling-Dekker except that a weak fermentation of galactose was obtained.

HANSENULA LAMBICA (Kufferath) Dekker (94).

Cells spherical, oval to elongate, ogive. Dimensions of cells from films on liquid wort $1.75-5\times5-24\,\mu$ at 1 and 3 days, $1.25-4\times3.5-28\,\mu$ at 10 days; from films on synthetic medium $1.75-5\times6-30\,\mu$ at 3 and 10 days, mostly pseudomycelia of elongate cells at 10 days. No sporulation obtained. Pseudomycelia of elongate cells on wort agar, blastospores spherical and oval. Films on liquid wort thin, smooth, thick sectors. Film drops in large segments. On synthetic medium thin, farinose. Sediment increases with time. 60 day wort gelatin giant colonies flat, slightly rugose, border undulate, dull, buff. 60 day wort agar slant convex, vesicular, slope slightly contoured, border

lobate-lobulate, glistening, periphery plumose, light buff. 30 day synthetic agar slant convex, rugose, border lobulate, dull, light ivory. Fermentation of glucose, fructose, mannose, galactose, maltose, sucrose, raffinose (1/3). Does not ferment xylose, arabinose, glycerol, mannitol or dextrin. Nitrate and nitrite assimilated. Forms very little ester. Ethyl alcohol utilized. Esculin and salicin hydrolyzed.

The characteristics of this species agree with those given by Custers (1940) for *Brettanomyces lambicus*. However, as the original description of this species was not available we shall retain it as a species of the genus *Hansenula*.

ZYGOHANSENULA CALIFORNICA Lodder (76, 96).

Cells spherical to oval at 1, 3 and 10 days in liquid wort and synthetic medium. Dimensions of cells $3.5-7 \times 3.5-7 \mu$. Isogamous copulation; spores Saturn-shaped, $1.5-2.35 \times 2-2.5 \mu$, 1-4per ascus. No sporulation obtained with culture 76. Films on liquid wort within 48 hours, thin, smooth. Sediment increases with time. No pseudomycelium. 60 day wort gelatin giant colonies flat, smooth, border slightly undulate, dull, buff. 60 day wort agar slants smooth, convex, slope contoured, border lobatelobulate, glistening, periphery slightly plumose, light buff. 30 day synthetic agar slant, smooth, glistening, light ivory. Ferments glucose, fructose, mannose only. Does not ferment galactose, maltose, sucrose, raffinose, xylose, arabinose, glycerol, mannitol or dextrin. Nitrate and nitrite assimilated (auxanogram method). Growth in synthetic medium very poor. Forms very little ester. Ethyl alcohol utilized. Esculin and salicin hydrolyzed.

The other cultures included in this investigation have been identified as follows.

Six cultures were identified as species of the genus *Pichia*. Three cultures have been identified as *Pichia fermentans* Lodder and one as *Pichia Chodati* (Zender) Dekker. Culture 40 differs from *Pichia fermentans* in its rugose film, rugose slant on synthetic medium and the formation of pseudomycelia in synthetic medium. It has therefore been designated as follows:

Pichia fermentans var. rugosa var. nov.

Cells spherical, oval and elongate, chains of elongate cells at 3 and 10 days in synthetic medium. Dimensions of cells from

films on liquid wort $1.75-3.5 \times 3.5-9 \mu$ at 1 day, $2.5-3.5 \times 5.25 14 \mu$ at 3 days, $1.75-3.5 \times 3.5-12 \mu$ at 10 days; from films on synthetic medium 2.3-4.7 \times 6.5-16 μ at 3 and 10 days. Pseudomycelia of elongate cells in liquid synthetic medium at 3 and 10 days. Pseudomycelia of elongate cells on wort agar, no blastospores observed. No conjugation immediately preceding ascospore formation; spores hat-shaped, $1.6-2 \times 2.2-3 \mu$, 4 per ascus. Films on liquid wort and synthetic medium within 24 hours; on liquid wort very rugose and thick, on synthetic medium smooth at 3 days, then becomes rugose. Slight sediment. 60 day wort agar slant raised, finely vesicular, border lobulate, dull, wood brown. 30 day synthetic agar slant convex, rugose. border lobulate, dull, light rose. Ferments glucose, fructose and mannose only. Does not utilize maltose, galactose, arabinose, salicin, phloridzin, a methyl glucoside, sodium pyruvate or erythitol. Nitrate, nitrite or succinimide not assimilated. No ester formation. Gelatin liquefied. Ethyl alcohol utilized. Esculin hydrolyzed.

Culture 103 differs from any of the described species of *Pichia* in its poor growth in synthetic medium and its formation of ester. This culture is designated as follows:

Pichia Kluyveri sp. nov.

Cells spherical, oval in liquid wort. Dimensions of cells from films on liquid wort $2-6\times 3.5-10\,\mu$ at 1, 3 and 10 days. Sporulation in 10 day old wort culture (15° Balling). No conjugation immediately preceding ascospore formation; spores hat-shaped, $1.5-1.75\times 2-2.5\,\mu$, 2-4 per ascus. No pseudomycelium. Films on liquid wort within 48 hours, rugose. 60 day wort gelatin giant colonies slightly rugose, flat, borders entire, dull, light grey. 60 day wort agar slant finely vesicular, flat, border lobulate, dull, cinnamon. Ferments glucose, fructose and mannose only. Does not utilize maltose, galactose or arabinose. Growth in synthetic medium very poor. Ammonium sulfate and peptone assimilated; nitrate, nitrite, urea or asparagin not assimilated (auxanogram method). Ester formed in grape juice and yeast juice with glucose. With ethyl alcohol slight sediment. Esculin hydrolyzed, salicin not hydrolyzed.

Six cultures were identified as belonging to the group Candida Krusei as defined by Langeron and Guerra (1938), two cultures belonging to the group Candida Guilliermondi of Langeron and Guerra, one culture as Brettanomyces bruxellansis Kufferath and

van Laer, and two cultures as species of the genus *Torulopsis*. One culture (77) is very similar to *Torulopsis californicus* Mrak and McClung (1940).

The following key has been formulated on the basis of this investigation. Observations made concerning variations in the cultures indicate, however, that this may prove to be only an elaboration of the work of Stelling-Dekker towards a more stable and reliable classification. The observations made concerning variation also indicate that a study of the homozygous or heterozygous nature of single cells or blastospores will be necessary before the limitation of species or varieties can be definitely established. At the present time it seems that future studies should be carried out using the methods employed by Snyder and Hansen (1940) in their studies of *Fusarium*.

KEY FOR THE SPECIES OF THE GENUS HANSENULA SYDOW

	The rot the branch of the oblive thingshould brown
1a.	Spores Saturn-shaped
b.	Spores hat-shaped
	Pellicle extremely thin and indistinct
b.	Pellicle well developed and distinct
3a.	Vigorous fermentation of glucose, sucrose and raffinose
	(1/3) only
b.	Vigorous fermentation of glucose, maltose; ferments
	sucrose slowly, galactose weakly; no fermentation of
	raffinose
c.	Vigorous fermentation of glucose, galactose, maltose,
	sucrose and raffinose (1/3) 4
4a.	Cells spherical or oval, pellicle thin on synthetic me-
	dium, no pseudomycelium
b.	Cells spherical, oval or elongate, pellicle well developed
	on synthetic medium, no pseudomycelium
	Cells predominantly spherical, oval, occasionally shortly
	elongate on synthetic medium, pellicle well developed,
	no pseudomycelium
	sphaerica
d.	Cells spherical, oval and elongate, pellicle well de-
_	veloped, pseudomycelium on synthetic medium 5
5a.	Pseudomycelium of elongate cells, no ogive cells
b.	Pseudomycelium of heteromorphic cells, no ogive cellsH. anomala var. heteromorpha
c.	Pseudomycelium of elongate cells, ogive cells in liquid
	wort
	KEY FOR THE SPECIES OF THE GENUS ZYGOHANSENULA LODDER
Spo	res Saturn-shaped, fermentation of glucose only Z. californica

DISCUSSION

The results of this investigation have shown that the species *H. saturnus*, *H. suaveolens*, *H. Ciferri*, *H. Schneggii* and *H. lambica* are sufficiently distinct to be retained. The species *H. anomala*, *H. anomala* var. *sphaerica* and *H. anomala* var. *longa* have also been retained but redefined on the basis of cell size in liquid synthetic medium.

The characteristics of the species *H. nivea*, *H. panis*, *H. anomala* var. *robusta*, *H. anomala* var. *productiva* and *H. javanica* are not sufficiently distinct from the above three species to continue their separation as species or varieties.

Two cultures were sufficiently distinct from the described cultures to justify the establishment of a new variety, *H. anomala* var. *heteromorpha*, due to their formation of a pseudomycelia of heteromorphic cells in synthetic medium. Twelve cultures on the basis of their very poor film formation and poor growth in synthetic medium justified the establishment of a new species, *H. subpelliculosa*.

The morphological studies of the strains of *Hansenula* showed that, with the exception of cell size, there is very little difference between the films, slant cultures, giant colonies, spore formation and pseudomycelia. *H. saturnus* is readily distinguished from the other species by its Saturn-shaped spores.

Cell size in synthetic medium was used, in preference to liquid wort, as this medium can be easily duplicated and therefore the differences that occur in wort and other natural media used by various investigators can be eliminated. *H. anomala* and its varieties can only be separated on the basis of their cell size. This is not entirely satisfactory as the cultures show considerable variability in their cell size in the same medium and in different media. For example, a number of cultures placed in *H. anomala* var. *sphaerica* on the basis of cell size in synthetic medium form elongate cells in liquid wort and occasionally in synthetic medium. However, until more detailed studies are made on this variability within the cultures it seems best for the present to separate *H. anomala* and its varieties on the basis of cell size in synthetic medium.

This variability was also observed in *H. Ciferri*. Spherical, oval and elongate cells were observed initially but during successive transfers on liquid wort the culture lost its ability to form elongate cells. Later a six month old agar slant was examined and a few elongate cells were observed. On transferring this culture to liquid wort spherical and oval cells were observed in the film and elongate cells and pseudomycelia of very elongate cells were found in the liquid and sediment.

Spore formation was observed in most cultures. With the exception of *H. saturnus* the spores were hat-shaped. Spore formation was obtained most readily with carrot wedges. The number of spores per ascus was variable and not only varied between the strains but in the same strain on different media. In some cases, where sporulation could not be obtained initially it could be induced by repeated transfers in grape juice, liquid wort, prune or cherry juice before transferring to carrot wedges or gypsum blocks. However, a few of the cultures lost their ability to sporulate during the culture in the laboratory and although repeated attempts have been made no sporulation could again be obtained.

The physiological condition of the culture also appears to play an important part in sporulation as it did not occur regularly on the media used. For example, sporulation was obtained within six days on carrot wedges after transfer from an actively growing culture at one time and at another time no sporulation was obtained within six weeks.

The slant cultures, giant colonies and films of the various cultures show some differences but as a whole are not suitable for the separation of species.

The pseudomycelia of all species except *H. saturnus* and *H. suaveolens* developed as long chains of elongate cells. Occasionally pyriform, clavate and other shaped cells were present, as in *H. anomala* var. *heteromorpha* where pseudomycelia of heteromorphic cells developed in synthetic medium. Budding may occur from any cell in the chain with the formation of a subsidiary chain, however the intersection of the branches usually occurs at cell junctions. The cells in these chains are loosely

held together and can be easily separated. Blastospores are formed and are spherical and oval.

With the formation of pseudomycelium the species of Hansenula show a very close relationship to the genus Candida as with the lack of sporulation the cultures could readily be placed in the species Candida pelliculosa as defined by Diddens and Lodder. Diddens and Lodder (1940) were able to show a close relationship between H. javanica and H. anomala and Candida pelliculosa.

The studies on the fermentation of sugars showed some differences. H. saturnus and H. suaveolens do not ferment galactose and maltose. H. Schneggii does not ferment raffinose, ferments sucrose slowly and galactose very slightly. H. anomala and its varieties, H. Ciferri and H. lambica, ferment glucose, fructose, mannose, galactose, maltose, sucrose and raffinose (1/3). H. subpelliculosa does not ferment galactose. Zygohansenula californica ferments glucose, fructose and mannose only.

The studies on the utilization of carbon compounds show some differences. H. saturnus and H. suaveolens were unable to utilize arabinose, galactose, maltose, phloridzin, dextrin, erythitol or α methyl glucoside. Culture 39 placed in H. anomala, cultures 8, 9, 10, 11, 55 and 58 in H. subpelliculosa did not utilize galactose and cultures 45, 48 and 50 in H. anomala var. sphaerica did not utilize α methyl glucoside. Ethyl alcohol, glycerol, mannitol, erythitol, dextrin, amygdalin, salicin, esculin, ethyl acetate, sodium pyruvate and xylose as well as the compounds mentioned above were utilized by all the other cultures. Lactose, inulin, starch, dulcitol, inositol, glycogen, acetone, isoamyl alcohol and methyl alcohol were not utilized by any of the cultures.

Acetic, citric, fumaric, lactic, malic, malonic and succinic acids were utilized by most of the species when the concentrations were not too high, e.g. 0.3 per cent. H. saturnus did not utilize malonic acid, H. suaveolens malonic and citric acid, and H. Ciferri acetic, citric, fumaric, malic and malonic acids. Succinic and lactic acids were the most readily utilized and acetic acid the least readily utilized. Adipic, butyric, caproic, crotonic, formic, glycollic, itaconic dl mandelic, maleic, mucic, oxalic, propionic

and tartaric acids were not utilized. Butyric, crotonic, maleic, and oxalic acids were toxic in concentrations of 0.2 per cent.

The studies on the utilization of nitrogen compounds showed that, with the exception of succinimide and guanidine the species of Hansenula show very little difference in their utilization. Glycine, dl alanine, β alanine, dl valine, dl leucine, l leucine, dl serine, l aspartic acid, d glutamic acid, d arginine, cysteine, cystine, dl phenylalanine, l histidine, tyrosine, tryptophane, dl α amino n valeric acid, dl norleucine, proline, glycyl-glycine, ethyl amine, n butyl amine, tyramine, urotropine, acetamide, succinimide, guanidine, urea, asparagin, allantoin, uric acid, uracil, betaine, peptone, yeast nucleic acid, ammonium sulfate, potassium nitrate and sodium nitrite were all utilized. cinimide was not utilized by H. saturnus, H. Schneggii, H. Ciferri and H. suaveolens, cysteine by H. Ciferri and guanidine by H. Schneggii, two cultures placed in H. anomala and nine cultures placed in H. anomala var. sphaerica. Sarcosine was only utilized by H. saturnus. Only 33 per cent of histidine and 50 per cent tryptophane were utilized. Comparing these results with those obtained by Thorne (1933) and Nielsen (1936, 1938) we see that the species of Hansenula are able to utilize nitrogen compounds as cystine, acetamide, allantoin, betaine and β alanine which were not utilized by the strains of Saccharomyces cerevisiae. Many of the cultures were also able to utilize both forms of the racemic mixtures and d arginine completely whereas Nielsen found that, with the exception of aspartic acid, asparagin and glutamic acid, his culture was able to utilize only half of the racemic mixture and half of d arginine.

The nitrogen assimilation by *H. subpelliculosa* and *Zygo-hansenula californica* was only shown by the auxanogram method as these two species grow very poorly in synthetic medium. None of the species studied other than *Hansenula* assimilate nitrate or nitrite.

The occurrence of slight growth and a change in pH is not a true indication of the ability of the organism to utilize the compounds. This is shown, for example, with H. saturnus and H. suaveolens with maltose and galactose as carbon sources, where there was a slight amount of growth and a definite change in

pH but quantitative determinations show that these compounds are not utilized. Nielsen (1936) has shown that the yeast can increase its solid matter up to three times the original amount without any utilization of the nitrogen compound.

The morphological studies on the cultures included in the genus Pichia and Candida Krusei showed that they are similar to the species of Hansenula in cell size, film formation, slant cultures, giant colonies and pseudomycelium formation. All strains of Pichia formed hat-shaped spores with a narrow brim. The physiological studies showed considerable differences. Pichia fermentans and variety rugosa, Pichia Kluyveri and Candida Krusei fermented glucose, fructose and mannose only. Only ethyl acetate and xylose were utilized. With the exception of Pichia Kluyveri they all utilized the organic acids except malonic acid as the species of Hansenula. Pichia Kluyveri and Candida Krusei formed ester.

SUMMARY

A morphologic and taxonomic study has been made of 100 cultures of yeast obtained as species of Hansenula from various sources in the United States, Europe, Asis and South Africa. This collection yielded 79 cultures of Hansenula, 6 of Pichia, 8 of Candida, 2 of Torulopsis, 2 of Zygohansenula and 1 of Brettanomyces. The cultures of Hansenula were placed into seven species and three varieties. They are H. saturnus, H. suaveolens, H. Schneggii, H. lambica, H. Ciferri, H. anomala and the varieties H. anomala var. sphaerica, H. anomala var. longa and H. anomala var. heteromorpha, and H. subpelliculosa. The species are differentiated by their fermentation, film, cell size, pseudomycelium formation and growth in synthetic medium. The varieties are differentiated by cell size in synthetic medium and pseudomycelium formation.

The cultures of *Pichia* studies were placed in the species *Pichia* Chodati, P. fermentans, P. fermentans var. rugosa and P. Kluyveri. The other organisms identified were Candida Krusei, C. Guilliermondi, Brettanomyces bruxellansis, Torulopsis californicus and Zygohansenula californica.

The observations made concerning variation, particularly in the species *H. anomala* and its varieties, indicate that a study of the homozygous or heterozygous nature of single cells will be necessary before the limitation of species or varieties can be definitely established.

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The writer takes this opportunity to express his appreciation for the helpful assistance, and courtesies extended him during the course of this investigation by Dr. Lee Bonar, Dr. E. M. Mrak, Dr. H. A. Barker, Dr. W. V. Cruess, Dr. M. A. Joslyn, Mr. B. L. Smith and Mr. H. J. Phaff.

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SOME ADDITIONAL SPECIES OF CERATOSTOMELLA IN THE UNITED STATES

Ross W. Davidson 1
(with 4 figures)

INTRODUCTION

In North America considerable attention has been given to the species of the genus *Ceratostomella* that stain wood (4, 10, 17, 20, and 23) and that cause plant diseases (1, 2, 3, 11, and 14). Such studies indicate the economic importance of the genus, but the present paper deals with a number of species that have been isolated from wood in the course of decay studies and so far as is known were not associated with pronounced discoloration or disease in the host substrata. The five species described here fall into two fairly distinct groups, which have been referred by some mycologists to separate genera. For the present they are being assigned to the genus *Ceratostomella* with an indication of the subgroup to which they belong.

DESCRIPTION OF THE SPECIES

 Ceratostomella (Ophiostoma) microspora sp. nov. (FIG. 1, H-K: FIG. 2, G-I)

Mycelium growing slowly in culture, remaining white; peri, thecia begin to form in about two weeks, maturing slowly, blacknearly spherical, 200–270 μ in diameter, thick walled; beaks occasionally two on a perithecium, 1.2–1.6 mm. long by 60–75 μ thick at base to 18–19 μ thick just below ostiole; no filaments around the ostiole, but in very mature condition hyphae spread slightly to form a funnel-like opening; asci elongate ovoid, small evanescent; ascospores not collecting in a globule at the ostiole but running down on the outside of the beak, light pinkish-brown in mass, hyaline under the microscope, minute, 1.5–2.5 \times 0.5 μ

¹ Latin descriptions of the new species included in this paper were prepared by Edith K. Cash, assistant mycologist, Bureau of Plant Industry, United States Department of Agriculture.

conidia borne singly on hyphae or around the apex of hyaline cephalosporium-like conidiophores, usually slightly curved, 4–10 \times 1.2–2 μ , hyaline. Growth rate: 5 mm. in 5 days.²

Mycelio in culturis lente crescenti, albo; peritheciis atris, sphericis, 200–270 μ diam., 1–2-rostratis; rostris longis, 1.2–1.6 mm., basi 60–75 μ , apice 18–19 μ crassis; ciliis ostiolaribus nullis; ascosporis parvis, hyalinis, 1.5–2.5 \times 0.5 μ ; conidiis hyalinis, elongatis, curvulis, 4–10 \times 1.2–2 μ .

Isolated from a chestnut stump, State College, Pennsylvania, October 8, 1932, and from the heartwood of *Quercus* sp. near Edinburg, Virginia, 1934.

This fungus differs from most of the others in the absence of well-defined bristles or cilia around the ostiole (FIG. 1, I). The perithecia develop very slowly and the beaks increase in length even after the ascospores are being ejected in abundance. The beaks always seem, to grow toward the light. Cultures with the necks all growing in the direction of a window on one side of the laboratory have been turned in the opposite direction and on increased growth they curved back toward the window again.

A dense white growth of aerial mycelium and conidiophores covers the surface of the substratum and usually persists even after the perithecia are mature. The mycelium of the substratum also remains hyaline (FIG. 2, *G-I*), except for the darkbrown hyphae covering the perithecia.

The absence of bristles around the ostiole and the fact that no Graphium stage is produced by cultures of this species separates it from C. Querci Georgevitch (5), C. merolinensis Georgevitch (6), and C. Fagi Loose (13). At first it was thought that it might be similar to C. mycophila Rick (18), which grows on Polyporus sp., but examination of a specimen collected by Rick disclosed that species to have persistent asci and light-brown allantoid Valsa-like ascospores.

2. Ceratostomella (Ophiostoma) stenoceras Robak? (fig. 1, A-C; fig. 2, C-E)

Mycelium growing slowly in culture, becoming dark brown, developing dark segments or remaining white; perithecia begin to form in 2 to 3 weeks and mature slowly, usually very numerous

² Throughout this study growth rate is recorded as average radial growth of mycelium on 2.5 per cent malt agar at room temperature of about 25° C.

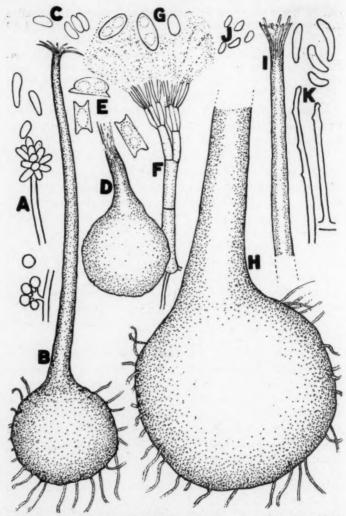


Fig. 1. A-C, Ceratostomella stenoceras Robak?—A, conidia and conidiophores, × 1500; B, perithecium, × 240; C, ascospores, × 1500. D-G, Ceratostomella leptographioides—D, perithecium, × 240; E, ascospores, × 2000; F, conidiophore, × 600; G, conidia, × 2000. H-K, Ceratostomella microspora—H, perithecium, × 240; I, tip of perithecial beak, × 240; J, ascospores, × 1500; K, conidia and conidiophores, × 1500.

black, spherical, 95–140 μ in diameter; beaks smooth, black, 370–650 μ long by 25 μ thick at base to 13 μ thick at ostiole; ostiole surrounded by a fringe of hyaline, slender, flexuous, filaments, 30–40 \times 1.2 μ ; asci small, globular, soon disappearing; ascospores hyaline, collecting at the ostiole in a hyaline spherical mass, 4–4.8 \times 1.5–1.8 μ ; conidia borne at the apex of hyaline conidiophores in cephalaosporium-like heads, elongate or nearly spherical, hyaline, one-celled, 4–8 \times 1.4–2 μ or 2.8–5 μ diameter. Growth rate 5½ mm. in 5 days.

Isolated from heartwood of living *Quercus* sp. decayed by *Stereum frustulosum* Fries, Hyde Park, N. Y., December 1933; from heartwood adjacent to 1-year-old injuries in trunks of *Quercus* sp. at Mt. Solon, Va., 1934; from *Quercus* sp., Edinburg, Va., and Southern, N. J., 1935; and from *Betula populifola*, Morristown, N. J., 1935; and others.

Typical cultures of this species on $2\frac{1}{2}$ per cent malt agar develop only a sparse growth of aerial mycelium and conidiophores which disappear as the cultures become darker and begin to develop perithecia. Other strains of the same or a closely related species do develop a heavier more persistent growth of conidiophore bearing mycelium (FIG. 2, E) and do not darken up as much as some of the so-called typical culture (FIG. 2, C). On Difco potato dextrose agar with .5 per cent malt added all cultures develop a heavier growth of aerial mycelium. Cultures held for several years and retransferred occasionally have lost all or some of the dark color (FIG. 2, D), but even entirely white cultures may develop some normal perithecia.

The perithecia of *C. stenoceras* develop slowly and sparsely on young cultures. They begin to form in 2 to 3 weeks and mature slowly, but (on recently isolated cultures especially) they continue to develop and in 4 to 6 weeks are present in great abundance. In this slow growth of mycelium and development of the perithecia it differs from many of the blue-staining species, such as *C. pilifera* (Fries) Wint., *C. pluriannulata* Hedge. (FIG. 2, *F*), and the lumber-inhabiting species *C. multiannulata* Hedge. & Davidson (4), but is similar in this respect to *C. microspora*.

The cultures obtained in this country are similar in some respects to *C. stenoceras* Robak (19), but the perithecia are smaller and develop more slowly. The ostiolar beaks are shorter on the

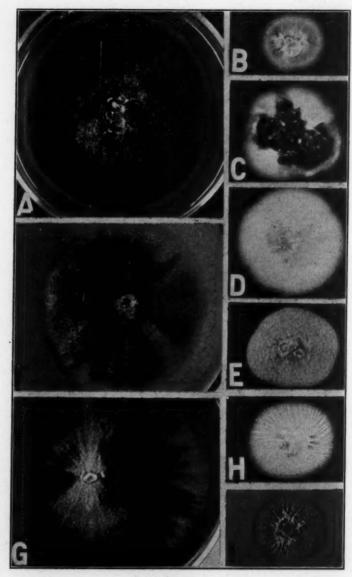


FIG. 2.

average than those described for C. stenoceras. On malt agar the growth is sometimes similar to zoned cultures described by Robak for his fungus, but usually the zonation is not pronounced. It differs from C. Castaneae Vanin & Solovjev (22) in its larger perithecia and shorter beaks. Also, ostiolar cilia of C. Castaneae are given as $14.7-20~\mu$ long while those of our fungus are $30-40~\mu$ long. C. Querci Georgevitch (5), C. merolinensis Georgevitch (6), and C. Fagi Loose (13) all have larger and longer beaked perithecia. They are also described as having Graphium imperfect stages whereas C. stenoceras has no such stage.

This is the most common *Ceratostomella* isolated from hardwoods, especially heartwood of *Quercus* sp. Many cultures of it have been studied and considerable variation observed, but for the present they are all being referred to *C. stenoceras* Robak.

3. Ceratostomella (Ophiostoma) minutum Siem. (fig. 3, F-H; fig. 4, A-C)

Mycelium remaining white, growing slowly; perithecia begin to form in 2 to 3 weeks and mature slowly, scattered, small, black, spherical, 60 to 80 μ diameter, rough; beaks of perithecia also rough, black, thick, cylindrical or tapering, short, 45 to 90 μ , sometimes longer; bristle-like cilia forming a tepee-shaped cone over the ostiole, light brown, pointed, about 12×1 –1.2 μ , and 8 to 12 in number; asci evanescent, not seen, but ascospores are arranged in groups of 8 within the perithecium; ascospores long, slender, slightly curved, pointed at the ends, about 10–15 μ long by 1 μ wide, hyaline, 1-celled; conidia borne at apex of hyaline cephalosporium-like conidiophores in globular bunches, 4–8 \times 2–4 μ , hyaline, 1-celled; growth rate, 4 mm. in 5 days.

Isolated along with a fast-growing species of *Cephalosporium* and a *Bacterium* from slightly stained sapwood of a dead pine trunk infested with *Monochamus titillator* Fabr. and several species of nematodes, collected near the District of Columbia,

Fig. 2. A, 10-day-old culture of Ceratostomella leptographioides; B, 10-day-old culture of Ceratostomella rostrocylindrica; C-E, 10-day-old cultures of Ceratostomella stenoceras Robak?—C, dark culture; D, white culture; E, culture with abundant aerial growth; F, 10-day-old culture of Ceratostomella pluriannulata Hedge.; G, 35-day-old (perithecia developed), and H and I, 10-day-old (perithecia not yet developed) cultures of Ceratostomella microspora; all \times 1. (Photographs by M. L. F. Foubert.)

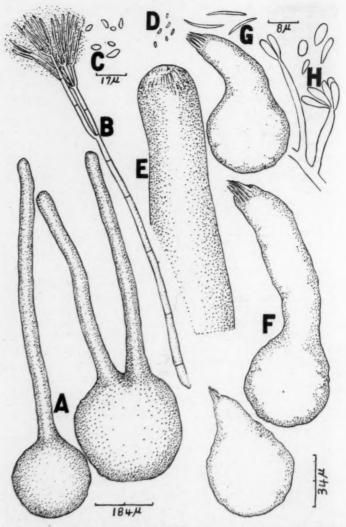


Fig. 3. A-E, Ceratostomella rostrocylindrica—A, perithecia; B, conidiophore; C, conidia; D, ascospore; E, tip of perithecial beak. F-H, Ceratostomella minutum Siem.—F, three perithecia; G, ascospores; H, conidia and conidiophores.

August 1934. It was also isolated from several of the *M. titillator* grubs that had been surface-sterilized.

Ceratostomella minutum differs strikingly from any other species known to the writer. The short thick perithecial necks topped by the compact conically arranged bristles (FIG. 3, F; FIG. 4, A & B) and the long narrow ascospores (FIG. 3, G) are outstanding features that separate it from other species. The American fungus is here considered the same as Siemaszko's (21) species although the perithecia studied by the writer are smaller. The American fungus was studied only in cultures on malt agar, as developed in association with the Bacterium (FIG. 4, C). Single-spore cultures did not develop perithecia.

Ceratostomella (Grosmannia) leptographioides sp. nov. (Fig. 1, D-G; Fig. 2, A)

Mycelium light-gray in culture, soon covered with conidiophores; perithecia forming in 4 or 5 days, maturing slowly, abundant, black, spherical, $100-150\,\mu$ in diameter; beaks short, $150-180\,\mu$ long by $35-40\,\mu$ thick at base to $20\,\mu$ at ostiole; cilia numerous, straight, bristle-like, hyaline, pointed at ends, $16-28\,\mu$ long; asci small, disappearing; ascospores hyaline, kidney-shaped surrounded by a gelatinous sheath, $6-7.5\,\times\,2.8-3.8\,\mu$ including sheath; conidiophores as in *Leptographium*, brown, septate, with hyaline brush-like branches at apex, $150-250\,\mu$ high by $4-7.5\,\mu$ thick; conidia borne at tips of hyaline branches, small, hyaline, $2-7\,\times\,1.5-3.5\,\mu$. Growth rate 13 mm. in 5 days.

Mycelio moderatim crescenti, griseo; peritheciis abundantibus, parvis, atris, sphericis, 100–150 μ diam.; rostris brevibus, atris, 150–180 μ longis, basi 35–40, apice 20 μ crassis; ciliis setiformibus, hyalinis, acuminatis, 16–28 μ longis; ascosporis reniformibus, hyalinis, in vagina gelatinosa vestitis, 6–7.5 \times 2.8–3.8 μ , vagina inclusa; conidiophoris ut in *Leptographio*, brunneis, septatis, apice multo ramosis, 150–250 μ altis, 4–7.5 μ crassis; conidiis parvis, hyalinis, 2–7 \times 1.5–3.5 μ .

Isolated from heartwood of stump of *Quercus* sp., Edinburg, Va., February 1934, and from specimen of decayed *Quercus* sp. stump from Ohio, 1936.

Two other species of this group are *C. penicillata* Grosmann (9) and *C. piceaperda* Rumbold (20), which have much larger and longer beaked perithecia and are faster growing. Goidanich (7) set up the genus *Grosmannia* for species of *Ceratostomella* having *Leptographium* conidial stages. He also described *G.*

serpens Goid., which is more closely related to *C. penicillata* and *C. piceaperda* than to this or the following species.

5. Ceratostomella (Grosmannia) rostrocylindrica sp. nov. (Fig. 2, B; Fig. 3, A-E)

Mycelium growing very slowly in culture, white or gray at first, finally becoming dark brownish gray, surface slimy, appressed, with very sparse aerial conidiophores and mycelium; perithecia develop slowly, maturing in 4 to 6 weeks, black, large, about 300 μ in diameter; beaks 400–600 μ long, black, sometimes 2 or 3 to a perithecium, cylindrical, and with no fringe of cilia around ostiole; ascospores small, 2–4 \times 1–1.6 μ , hyaline; conidiophores as in *Leptographium*, single or grouped, brown, septate, relatively small, 100–350 μ \times 2.5–5 μ ; conidia on penicillate branches at apex of conidiophores, globose or elongate, 2–6 \times 1–3.5 μ . Growth rate 2–3 mm. in 5 days.

Mycelio in culturis lentissime crescenti, griseo; peritheciis tarde maturantibus, stris, magnis, 300 μ diam.; rostris interdum 2–3, longis, cylindricis, atris, 400–600 μ longis, ciliis nullis; ascosporis parvis, hyalinis, 2–4 \times 1–1.6 μ ; conidiophoris ut in *Leptographio*, brunneis, septatis, apice multo ramosis, 100–350 \times 2.5–5 μ ; conidiis hyalinis, parvis, 2–6 \times 1–3.5 μ .

Isolated from heartwood of *Quercus* sp. from Connecticut, September 1936.

Growth is much slower than that of any other species of the group (FIG. 2, B). Conidiophores are smaller and less abundant than for any described species of Leptographium. This and the preceding species grow more slowly and differ from the non-perithecial species Leptographium Lundbergii Lagerberg & Melin (12) in general growth characteristics. A number of forms having no perithecial stage have been isolated from pine wood in this country, but in general most of them fit the description of L. Lundbergii fairly well, except for their longer conidiophores, and are more nearly similar to conidial stages of Ceratostomella penicillata and C. piceaperda than to either of the two species of the group described here.

DISCUSSION

Single-spore Cultures

The writer has not made a study of single-ascospore cultures of the new species described in this paper, but a few single conidial cultures were obtained. Single conidial cultures of *C. stenoceras* did not develop in an entirely normal manner, but some mature ascospore-bearing perithecia developed in five of eight such cultures. The other three cultures contained only immature perithecia. None of these cultures developed the black crustose

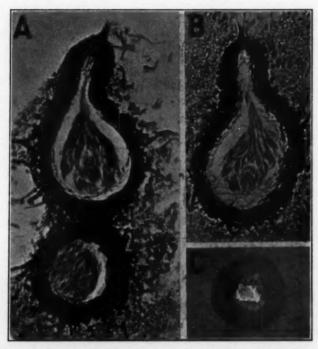


Fig. 4. Ceratostomella minutum Siem. A and B, photomicrographs of sections through mature perithecia, × 600; C, 10-day-old culture with bacterial contaminant, × 1. (Imbedding and sectioning by Dorothy Blaisdell Vaughn. Photomicrographs and photograph by M. L. F. Foubert.)

concentric zones that were frequently formed by the original isolations. The mass isolates of *C. stenoceras* sometimes do not develop perithecia very readily on malt agar, so the fact that three of the single conidial cultures did not have mature perithecia does not prove that they were incapable of producing fertile perithecia.

All of the single conidial cultures of *C. microspora* obtained developed mature perithecia, as did those of *C. leptographioides*.

Taxonomic Considerations

Melin and Nannfeldt (15) have pointed out the differences between species originally described in the genus Ceratostomella and the numerous species later described as having ephemeral asci and also placed in the same genus. The writer agrees that the species that Nannfeldt and Melin place in Ophiostoma are probably generically distinct from Ceratostomella vestita Sacc. and related species, but can not agree with his statement that C. penicillata "can not be included in it (Ophiostoma), as it lacks the fringe of ostiolar cilia." If the ostiolar cilia are to be considered such an important character, C. leptographioides would have to be placed in a separate genus from C. penicillata along with species more distantly related.

It is the writer's opinion from a study of a considerable number of species, some of which belong in every known group of the genus *Ceratostomella* (except the *C. vestita* and *C. cirrhosa* group), that neither the ostiolar filaments nor any other perithecial character can be used in separating the groups of the genus.

Our present knowledge of this Ceratostomella complex indicates that conidial stages are much more reliable for placing the species in their natural groups. The endoconidial group has already been separated by the writer (4) and placed in the genus established by Münch (16), and no doubt the Leptographium forms should also constitute a separate genus, as was concluded by Goidanich (8). The remaining species should be more clearly defined by further investigations, but probably will be considered a heterogeneous mixture of closely related groups and placed in the genus Ophiostoma. It might be pointed out, however, that whereas many species of the Ophiostoma, Grosmannia, and Endoconidiophora groups have been carefully studied in pure culture, none of the species of Ceratostomella having persistent asci has, so far as the writer is aware, been studied in culture. Therefore, it is possible that there may not be distinct cultural differences between them. A study of C. vestita and related species with persistent asci seems necessary for a better understanding of their relationship to the other groups of species.

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SOME NEW AND INTERESTING FUNGI FROM MOUNT SHASTA

LEE BONAR AND WM. BRIDGE COOKE

During the past few summers several interesting species of fungi have been collected by the junior author on Mount Shasta, situated in south central Siskiyou County in northern California. Studies made on some of these fungi have found them to be heretofore unreported, others are new to North American records. Many of the microscopical observations to be reported were made by the senior author.

PLEOSPORA AND LEPTOSPHAERIA

A number of collections of species in these two genera have been made. They occur on dead fragments of herbaceous plants. Above-ground portions of perennial herbs, both monocots and dicots, are subject to rapid decay. This takes place during two successive winters. During the first winter after the plant has bloomed and fruited the plant is covered with snow. After the snow has melted, species of these two genera, as well as species of other Ascomycetes, are found on stems of any species observed. During the second winter decay is completed since no remains are found at its close. So far as collections made to date show species of *Leptosphaeria* predominate on monocot hosts while species of *Pleospora* predominate on dicots.

On overwintered parts of various grasses, sedges and rushes have been found material of what might be referred to three species of *Leptosphaeria*. Karsten described three species of *Leptosphaeria* from similar hosts on Spitzbergen: *L. vagans* on grasses, *L. caricinella* on sedges and *L. junciseda* on rushes. Our material corresponds with these three species. However, on closer examination the three species appear to be identical, both from the Saccardian translation of the type description and from the material at hand. This also indicates that too close a dependence on the host cannot indicate lines between species in

this genus. Comparative tables listing species of this genus found on Gramineae, Cyperaceae and Juncaceae also indicate a lack of specific differentiation in this group based on the host relationship.

Comparative lists of all species of *Pleospora* listed in Saccardo indicate that specific differences in this genus are based in many cases on host relationships which, in the case of fungi growing on dead herbaceous matter, appear to be of little importance. From a wide range of hosts, specimens of Pleospora permunda (Cooke) Sacc. have been obtained. Should the common practice of including minor variations of spore size on different hosts be followed here, a number of species or varieties could be erected. At present it appears, however, that fewer species, rather than more, should be the rule in this and related genera. Pleospora is a genus which was based, among other morphological characters, on its muriform spores. It was segregated into Clathrospora on the basis of the spores in certain species being septate in only two dimensions, spores which appear like those of *Pleospora* in one plane and like those of Leptosphaeria in the other, producing flattened spores. It was further segregated into Catherinia on the basis of certain species which possessed hyaline spores. We have not found species of Catherinia on Mount Shasta, but because certain Catheriniae possess dilute chlorinous to even pale yellow spores, and some Pleosporae possess spores as pale as chlorinous it is suspected that there is no generic difference here. The difference between muriformness of a two- or three-dimensional quality appears to be negligible when segregating portions of Pleospora; thus Clathrospora, in which P. permunda was described by M. C. Cooke, appears to be a superfluous genus. Most Pleospora species with 3, 4, 5, 6 and 7 longitudinal septae appear to be reported as septate in only two dimensions.

SPECIES IN OTHER GENERA

METASPHAERIA SEPALORUM Vleugel.

Perithecia crowded in black tuberculate masses, becoming superficial, globoid, nested in a cottony black subiculum and only barely visible, not stromatic; walls hairy, thin, flexuous, black, tending to separate when masses are crushed; ostiole poroid, not papillate; perithecia $290-325\,\mu$ in diameter, subepidermal in

origin; asci 8-spored, 96–120 \times 15–19 μ ; paraphyses flexuous, simple to anastomosed and branching; spores 3-septate, with hyaline walls and light brown contents, appearing completely hyaline in phloxine, 30–33 \times 7–9.5 μ (LB), 26.2–30.5 \times 7–9.5 μ (WBC).

On perianth segments of *Juncus Parryi* Engelm. in the summer of the year following the blooming period. *WBC 10303*, Mount Shasta, The South Gate, 8000 feet.

Bifusella acuminata (Ellis & Ev.) Bonar & W. B. Cooke, comb. nov. (*Duplicaria acuminata* Ellis & Ev. Proc. Acad. Phil. **1895**: 429.)

Hysterothecia subcuticular in origin, sessile, black, shining, smooth, rectangular with rounded corners, 0.75–1 mm. long, opening not evident in most, a mere slit in one or two; wall carbonized, 25 μ thiek above, thinner below, no distinct labia; asci 8-spored, 115–130 \times 18–20 μ ; paraphyses few, simple contorted or spiraled above, not always the full length of the asci; spores hyaline, 28–33 \times 3.5–4 μ , not including the sheath (soluble in KOH) which is as thick as the dumbbell-shaped spore and hyaline.

On *Juncus Parryi* Engelm. culms. *WBC 10184*, near Horse Camp, Mt. Shasta, 8000 ft., and *WBC 10303* in the South Gate, Mt. Shasta, 8000 ft.

Lophodermium Phloxii Bonar & W. B. Cooke, sp. nov.

Hysterotheciis epiphyllis, nigris, subepidermalibus, acutis fuseoideoellipticus, 0.75-1.25 mm. \times 500–600 μ ; labiis carbonaceis, agglutinatis epidermide; periphysibus obscure; ascis 8-sporis, clavatis, apice subacutis, basi brevistipitatis, $120-130 \times 12-14.5 \mu$; paraphysibus filiformibus, apice vix inflatis, simplicibus, $3-4 \mu$, plus minusve conglutinatis et epithecium formantibus; sporidiis fasciculatis, filiformibus, unicellularibus, subhyalinis, 55–70 \times 1.5–2.5 μ , in muco immersis.

Hysterothecia on leaves, black, shining, acute fusoid-elliptic, 0.75–1.25 mm. \times 500–600 μ ; subepidermal in origin; labia heavily carbonized with involved epidermis, 130 μ thick; periphyses gelatinized and indistinct; basal layer parenchymatic, carbonized, 25–30 μ thick, this overlaid by conspicuous, subhyaline, subhymenium; asci clavate, symmetrical, subacute at tip, tapers toward short stalk, 120–130 \times 12–14.5 μ , 8-spored, spores straight in ascus; paraphyses simple, flexuous, enlarged at tip to 3–4 μ , somewhat gelatinized and forming an epithecium; ascospores

straight, filiform, slightly enlarged above, 1-celled, subhyaline, $55-70 \times 1.5-2.5 \mu$, encased in thin hyaline gelatinous sheath.

On *Phlox Douglasii* Hook. *WBC 10185*, on moist flat at Horse Camp, Mt. Shasta, 8000 ft. Possibly this fungus is associated with *Macrophoma cylindrospora* previously reported from the same colony of host plants but not found in 1938 when this collection was made.

Phyllosticta Fritillariae Bonar & W. B. Cooke, sp. nov.

Pycnidiis dense gregariis, nigris, contextu laxiuscule cellulose, 90–125 μ in diam., sporulis bacillaribus, 1.5–1.9 \times 2.3–2.5 μ ; ostiolo obscuro.

Pycnidia thick-walled, densely gregarious, black, covering entire plant and blackening it on both sides of leaves as well as on stems and petioles; tissues of plant filled with brown hyphae with cells $10-20 \times 3.5-4 \,\mu$; cells of outer layers of pycnidia obovate to ovate, $6-8 \times 4 \,\mu$; pycnidia $90-125 \,\mu$ in diam.; spores bacillar, $1.5-1.9 \times 2.3-2.5 \,\mu$; ostiole present but indistinct.

On Fritillaria atropurpurea Nutt. WBC 15583, Wagon Camp, Mt. Shasta, 5700 ft. Two plants in a large colony of the host were infected. Infection resulted in dwarfing of the infected plants. In early stages the fungus appears as pale brown spots on straw colored leaves. No spores are associated with this phase.

There appear to be no described species of *Phyllosticta* on *Fritillaria*. Our fungus shows characters close to those of *P. hispida* Ellis & Dearness on *Smilax* in Eastern Canada. The symptoms of the latter fungus on parts of *Smilax* leaves would apply to those on our whole plant. Because of the nature of the present species concept in the form genus *Phyllosticta* it seems best, because of the geographic and host discontinuity of these two fungi, to retain them as separate species until further studies prove otherwise.

PHYLLOSTICTA MONARDELLAE W. B. Cooke in Mycobiota of North America 70.

Spots without definite margins, finally covering the entire leaf; leaf becoming brown; pycnidia black-punctate, separate, rarely 2–3 together, not confluent, spherical, not flattened by mutual pressure, hypophyllous, black, 60–120 μ in diameter; spores hyaline, rod-shaped, 1–1.5 \times 4–5 μ .

On Monardella odoratissima Benth. WBC 13404, near Wagon Camp, Mt. Shasta, 6000 ft. There appear to be no hitherto reported species of Phyllosticta growing on species of Monardella.

Phyllosticta nigrescens Bonar & W. B. Cooke, sp. nov.

Maculis ochraceis, margine olivaceis, extendentibus ad omne folium, denique nigrescentibus; pycnidiis sparsis, punctiformibus, epiphyllis, membranaceis, $100-130~\mu$ diam.; ostiolo poroso; sporulis hyalinis, bacilliformibus, $5-6\times1.5-2~\mu$.

Spots light tan, with olivaceous margin, spreading from tip or margin to involve entire leaf, finally becoming black; pycnidia scattered, single, epiphyllous, not visible below; thin-walled, 100–130 μ in diam.; ostiole poroid or slightly papillate; spores 1-celled, hyaline, bacilliform, 5–6 \times 1.5–2 μ .

On Viola purpurea Kellogg. WBC 13403, above Wagon Camp, Mt. Shasta, 6000 ft. On Viola Sheltonii Torr., collected by J. P. Tracy on Grouse Mountain, Humbolt Co., Calif.

Septoria shastensis Bonar & W. B. Cooke, sp. nov.

Maculis ochraceis, demum bruneis et extendentibus ad omne folium, pycnidiis sparsis, globosis, membranaceis, $100-150~\mu$, ostiolo epiphyllo; sporulis saepe paulum curvatis, plerumque sinuatis, 1-3-septatis, subhyalinis ad dilute brunneis, $20-38 \times 2.8-3.8~\mu$.

Pycnidia evenly scattered in leaf; leaf finally turns brown from tip or margin to involve entire leaf; pycnidia globoid, $100-150~\mu$, wall distinct all around but membranous, showing on both surfaces but openings epiphyllous; spores usually somewhat curved, mostly sinuous, 1-3-septate, dilute brown or subhyaline, $20-38~\times~2.8-3.8~\mu$; spore tips blunt rather than acicular.

On Aster shastensis Gray. WBC 15601, in chaparral along the Memorial Highway, Mt. Shasta, 4500 ft.

Several species of Septoria have been recorded on Aster spp. Of these Septoria tharpiana Trott. (S. angularis Tharp) appeared to be most closely related. However, on examination of type material of this species, kindly loaned by J. A. Stevenson, Mycological Collections, Bureau of Plant Industry, S. tharpiana was found to be quite different from the Mount Shasta material. S. tharpiana has longer, more slender spores and pycnidia in definite angular spots. S. astericola Ellis & Ev. has rounded or ovate rather than angular spots, while S. atropurpurea Peck has definitely purple spots. Again in these species the spores are different.

OLLULA PEZIZOIDEA Lév. Ann. Sci. Nat. IV 20: 299. 1863. (Siroscyphellina Arundinacede Petrak, Ann. Myc. 21: 255. 1923.)

Fruiting bodies 2–6, reddish flesh-colored, crowded erumpent in old leaf scars; shape irregular from crowded position or flattened globoid, up to 1 mm. in diameter; with a wide opening at top; fruiting bodies separate, not on a stroma common to clusters; conidiophores crowded around the walls of the fruiting body, branched, hyaline; conidia 3–5 \times 1–1.5 μ , hyaline, 1-celled.

On a twig of Abies magnifica var. shastensis Lemmon. WBC 15726. Near Horse Camp, Mt. Shasta, 8000 ft.

The material agrees with the descriptions of this species except that it is erumpent rather than superficial and that each fruiting body has its own pseudoparenchymatic stromatic base rather than such a base being common to several fruiting bodies.

RAMULARIA OBDUCENS Thuem.

Material referred to this species was collected on a colony of *Pedicularis densiflora* Benth. (*WBC 15502*, June 1941). The colony of the host which was growing along a roadside on the outskirts of Mount Shasta City, formerly Sisson, was heavily infected. The only previous report of a species of *Ramularia* parasitizing a species of *Pedicularis* in the United States was that of a collection made in 1925 at approximately the same location—Sisson, California.

Material of these species is deposited in the herbarium of the University of California as well as that of the junior author (at the University of Cincinnati). In addition duplicates of some of these species are at the New York Botanical Garden, the Mycological Collections of the Bureau of Plant Industry and the Farlow Herbarium. The junior author wishes to take this opportunity to thank the senior author for the use of laboratory facilities at the Herbarium of the University of California; he also wishes to thank John Thomas Howell for assistance with preparation of the latin diagnoses.

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AMERICAN RUSTS OF PANICUM, PASPALUM AND SETARIA

GEORGE B. CUMMINS
(WITH 24 FIGURES)

This paper presents the results of a taxonomic study of 14 species of the Uredinales parasitic upon hosts belonging to the genera *Panicum*, *Paspalum*, and *Setaria*. The rusts occur in the tropical and subtropical regions of North and South America. No attempt is made to account individually for the necessary changes in identification. In the case of exsiccati, however, the name of the set, and the number and name under which the rust was issued are given following the collector's name and number. Descriptions are given, together with synonymy. Where adequate material made it possible, photomicrographs of the teliospores of type specimens provide the illustrations.

Perhaps no group of rusts has been more confusing than that on grasses of the tribe Paniceae. This has been due to the scarcity of telia or to a failure to recognize their presence, and to the frequent comingling of more than one species in a single collection. Failure to recognize the presence of telia occurred in species whose telia are small and covered by the epidermis, as in Puccinia dolosa, P. circumdata, P. catervaria, Uromyces leptodermus and U. Puttemansii. Comingling of more than one species was primarily responsible for the confusion of Angiopsora compressa and P. dolosa with P. substriata, P. Puttemansii with P. levis, and led to the conception that P. paspalicola (P. tubulosa) was a species characterized by variable uredia. The variability in paraphyses and in the size and pigmentation of the urediospores, described for P. tubulosa (6), resulted from an attempt to include several species under a single name. Thus, the incurved, thick-walled paraphyses and nearly colorless urediospores be-

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longed to A. compressa, the hyphoid paraphyses belonged mainly to P. dolosa, and the telia belonged to P. substriata.

The rusts discussed in this paper are divisible into two groups. In the first the telia are small, inconspicuous and remain covered by the epidermis. In the second group the telia early rupture the epidermis and produce pulvinate and usually conspicuous sori. The aecial stage is known only for *P. substriata*.

SPECIES WITH INDEFINITELY COVERED TELIA

UROMYCES LEPTODERMUS Sydow, Ann. Myc. 4: 430. 1906. (FIGS. 7, 8.)

(Uredo Panici P. Henn. Hedwigia 43: 165. 1904; Puccinia
(?) panicicola Arth. Bull. Torrey Club 34: 586. 1908;
Uredo Eriochloae Speg. Anal. Mus. Nac. Buenos Aires 19: 319. 1909; Uredo eriochloana Sacc. & Trott. Syll. Fung.
21: 810. 1912; Nigredo leptoderma Arth. N. Am. Flora 7: 224. 1912; Uredo Panici-maximi Rangel, Arch. Mus. Nac. Rio de Janeiro 18: 160. 1916.)

Aecial stage unknown. Uredia amphigenous, elliptic or oval, 0.2–0.5 mm. long, cinnamon-brown, the epidermis opening widely by longitudinal rupture; urediospores broadly obovoid or broadly ellipsoid, $(20-)23-27 \times (25-)27-33(-35) \mu$; wall $1.5-2 \mu$ thick, cinnamon-brown, closely and rather finely echinulate; pores 3, equatorial. Telia amphigenous, scattered, oval or oblong, 0.2–0.4 mm. long, blackish, remaining covered by the epidermis; teliospores variable due to pressure in the compact, covered sori, angularly globoid or obovoid, $16-21 \times 19-27 \mu$; wall light chestnut- or golden-brown, uniformly $1-1.5 \mu$ thick, smooth; pedicel colorless, usually shorter than spore, rather fragile.

MATERIAL EXAMINED: Eriochloa annulata Kunth: ARGENTINA: Spegazzini (type of Uredo Eriochloae Speg.). E. Lemmoni Vasey & Scribn.; Mexico: Holway 3199. E. polystachya H.B.K.; VENEZUELA: Kern & Toro. E. punctata Ham.; TRINIDAD: Seaver 3193. E. subglabra (Nash) Hitchc.; PUERTO RICO: Earle 359; Seaver & Chardon 1306; Stevens 7605; Stevenson 3938; Whetzel, Kern & Toro 2125, 2205, 2206, 2353; Whetzel & Olive 398, 399, 400, 401, 402, 403, 404. Panicum barbinode Trin.; CUBA: Baker (Barth. Fungi Columb. 2671) (type of Puccinia panicicola Arth.); Britton & Wilson 14715, 15357; Earle 820;

Holway: Horne: Johnston 425; EL SALVADOR: Standley 19677; GUATEMALA: Holway 12: Kellerman 5364; MEXICO: Holway 3045 (Barth, N. Am. Ured. 857); PANAMA: Bethel; PERU: Holway 790; Rose 18723; PUERTO RICO: Hioram 360; Kern & Toro 37, 44; Stevens 350, 350 bis, 447, 480, 4560, 7122, 7168, 7199; St. Croix: Seaver 880; U. S. A.: Arthur; Bessey 65. P. maximum Jacq.; Brazil: Holway 1012 (Reliq. Holw. 101 as P. tubulosa), 1033 (Relig. Holw. 103 as P. levis); Rangel 749 (type of Uredo Panici-maximi Rangel); GUATEMALA: Standley 64716. P. purpurascens Raddi; U. S. A.: Clover 1511. P. texanum Buckl.; U. S. A.: Shear. Setaria geniculata (Lam.) Beauv.; CUBA: Britton & Wilson 15439; Jennings 154; Johnston 483, 558, 762; Shafer 11795; JAMAICA: Britton 1659; PANAMA: Bethel; Carleton 23; PUERTO RICO: Whetzel, Kern and Toro 2351, 2352; Whetzel & Olive 438: Stevens 9182: U. S. A.: Hitchcock 512. S. verticillata (L.) Beauv.; BERMUDA: Brown & Britton 116, 302; VENEZUELA: Toro 38.

In a recent paper Thurston (18) pointed out the differences between *U. leptodermus* and *U. costaricensis* Syd. He concluded that *U. costaricensis* should be maintained as a species and that it is restricted to *Lasiacis*, while *U. leptodermus* occurs on *Panicum*. He cited two North American collections, both on *P. barbinode* and both with telia.

In the present study telia and teliospores which agree with those of *U. leptodermus* were found on *Eriochloa subglabra* from Puerto Rico (Earle 359, Whetzel & Olive 401), on Panicum barbinode from Cuba (Baker 7113, Horne s.n., Johnston 425), El Salvador (Standley 19677), Guatemala (Holway 12, Kellerman 5364) and Mexico (Holway 3045), on P. purpurascens from Texas (Clover 1511), on a tall grass from the Dominican Republic (Chardon 1137) and on Setaria geniculata from Cuba (Shafer 11795). The specimens on Setaria and Eriochloa were found under P. substriata and were so published in the North American Flora. Arthur first (3) cited Eriochloa as a host under P. substriata in 1917 and later (5, 6) placed the concerned rust names in the synonymy of the species.

Only one collection on Setaria was seen with telia and, since there is some variation in the uredial collections, some of the

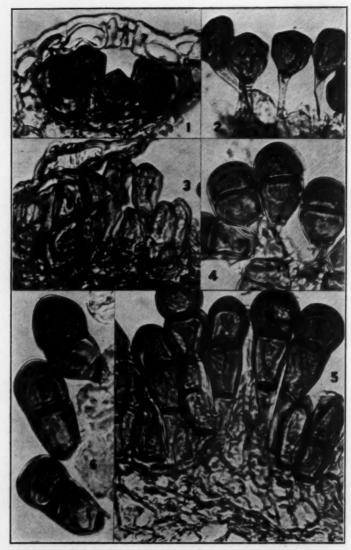


Fig. 1, free-hand section of a telium of *Uromyces sepultus* Mains (= *U. Puttemansii* Rangel) on *Setaria tenax* (from type); 2, teliospores of *U. sepultus* (from type); 3, free-hand section of a telium of *Uromyces niteroyensis* Rangel.

specimens may belong elsewhere. The urediospores of Uromyces Setariae-italicae (Diet.) Yosh., for example, are generally similar to those of U. leptodermus but no teliospores with the wall thickness of that species have been found in America. Arthur (6, p. 746) placed U. Setariae-italicae in the synonymy of U. leptodermus. The uredia of U. niteroyensis (= U. Puttemansii) which Arthur (l.c.) also placed under U. leptodermus are longer covered by the epidermis and the urediospores are larger than in U. leptodermus, in addition to the apically thickened wall of the teliospores of the former. In Puccinia catervaria the urediospores are smaller and have four pores, while in P. Chaetochloae the spores are larger and remain more persistently covered by the epidermis. Although Uredo Panici-maximi is given as a synonym, as was done by Arthur (l.c.), it is somewhat doubtful whether this is correct. In spite of the characters pointed out above, it will remain difficult to identify uredial collections and it is probable that the last word remains to be said concerning the morphological limits of U. leptodermus.

No aecial stage has been demonstrated for *U. leptodermus* and the only clue to a possible alternate stage is provided by Kern (10) who writes: "Field evidence indicated a possible connection between the rust on *Eriochloa polystachya* and the *Aecidium Serjanae* (Kern & Toro 1751)."

UROMYCES PUTTEMANSII Rangel, Arch. Mus. Nac. Rio de Janeiro 18: 159. 1916. (FIGS. 1-3.)

(Uromyces niteroyensis Rangel, Arch. Mus. Nac. Rio de Janeiro 18: 160. 1916; Uromyces sepultus Mains, Carnegie Inst. Washington Publ. 461: 99, 1935.)

Aecial stage unknown. Uredia amphigenous or mainly hypophyllous, scattered, elliptic, 0.2–0.6 mm. long, cinnamon-brown, the epidermis opening by a longitudinal slit or circumcisally, the epidermal cap then semi-persistent; paraphyses mainly peripheral

⁽⁼ U. Puttemansii) on Setaria sp. (from type); 4, teliospores of Puccinia substriata Ellis & Barth. on Paspalum paniculatum (from Holway 1679); this collection was closely associated in the field with Aecidium tubulosum; 5, free-hand section of a telium of P. substriata on Paspalum setaceum (from type); 6, teliospores of Puccinia Pilgeriana P. Henn. (= P. substriata) on Paspalum sp. (from type). × 700.

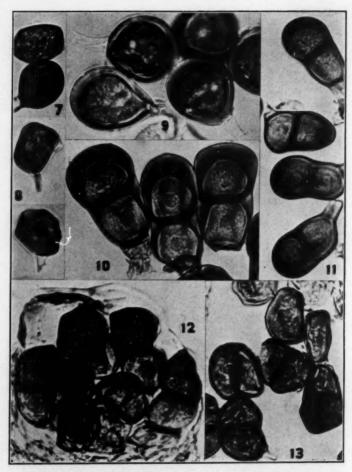


Fig. 7, teliospores of Uromyces leptodermus Syd. on Panicum barbinode (from Kellerman 5364); 8, teliospores of U. leptodermus Syd. on Eriochloa subglabra (from Whetzel & Olive 401); 9, amphispores (?) of Puccinia substriata? on Paspalum trachycauleon (from Tamayo 3767); 10, teliospores of Puccinia araguata Kern on Paspalum microstachyum (from type); 11, teliospores of Puccinia Huberi P. Henn. on Panicum trichoides (from Whetzel & Olive 414); 12, free-hand section of a telium of Puccinia dolosa Arth. & Fromme on Paspalum tenellum (from type); 13, teliospores of Puccinia circumdata Mains on Panicum fasciculatum (from type). × 700.

and clavate, yellowish, thin-walled, inconspicuous; urediospores obovoid or ellipsoid; $20\text{--}27 \times (26\text{--})29\text{--}38(-42)\,\mu$; wall $1.5\text{--}2\,\mu$ thick, cinnamon- or dark cinnamon-brown, prominently echinulate; pores 3, perhaps rarely 2 or 4, equatorial. Telia mainly hypophyllous, loosely grouped or scattered, oblong or linear, $0.2\text{--}2.0\,$ mm. long, blackish brown, remaining covered by the epidermis; teliospores variable due to pressure in the compact, covered sori, mostly obovoid, commonly angularly so, $14\text{--}20 \times (19\text{--})22\text{--}27(-30)\,\mu$; wall chestnut-brown, $0.5\text{--}1\,\mu$ thick at sides, thickened at apex to $1.5\text{--}2.5\,\mu$, smooth; pedicel persistent, usually shorter than spore, pale yellowish or golden.

MATERIAL EXAMINED: Setaria caespitosa Hack. & Arech.: URUGUAY: Holway 2016. S. leiantha Hack.; ARGENTINA: Holway 2035. S. paniculifera (Steud.) Fourn. (Chaetochloa sulcata Hitchc.); PANAMA: Carleton 16; Johnston. S. poiretiana (Schult.) Kunth; BRAZIL: Holway 1720. S. rariflora Mikan.; BRAZIL: Holway 1090. S. setosa (Sw.) Beauv.; Cuba: Rugel 880. S. tenax (Rich.) Desv. (S. onurus Griseb.); BRAZIL: Holway 1013, 1474 (Reliq. Holw. 102, 119 as U. leptodermus); BRITISH HONDURAS: Mains 4029; Cuba: Britton & Wilson 29; Johnston 301; Shafer 3020; Taylor 232; JAMAICA: Harris 12167; MEXICO: Swallen 2440 (type of U. sepultus Mains). S. sp.; BRAZIL: Rangel 1172 (type of U. niteroyensis Rangel).

Holway's South American collections in the above list were reported by Arthur (5) as *U. leptodermus*, under which he cited *U. niteroyensis* as a synonym. He discussed *U. Puttemansii* and *U. Panici-sanguinalis* in connection with *U. leptodermus* but reached no conclusion concerning their identity. Mains (*l.c.*) pointed out Arthur's error, with regard to Reliquiae Holwayanae nos. 102 and 119, when he published *U. sepultus*. The North American collections were separated from *Puccinia substriata*. In the 18 specimens studied telia were found on 11, including the type of *U. niteroyensis*. There appear to be no constant or substantial differences in the morphology of the various collections.

Uromyces Puttemansii is believed to be the correct name although this belief is based upon Rangel's description and figures (l.c., pl. 5, figs. 6-10) and not upon an examination of the type, which was not available. Rangel did not designate the type specimen and cited as hosts Setaria asperifolia and Panicum

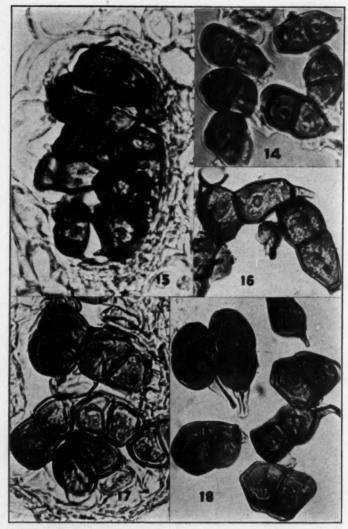


Fig. 14, teliospores of Puccinia Puttemansii P. Henn. on Panicum sp. (from type); 15, free-hand section of a telium of Puccinia Chaetochloae Arth. on Setaria macrosperma (from type); 16, teliospores of P. Chaetochloae on Paspalum floridanum (from Bartholomew 7608); 17, free-hand section of a telium of Puccinia catervaria Cumm. on Setaria geniculata (from type); 18, teliospores of P. catervaria (from type). × 700.

melinis, in that order. The numbers of these collections are 1211 and 1212, given in that order and both from Paqueta, Rio de Janeiro, June 1914. One would assume that no. 1211 would apply to the Setaria but there is a specimen (no. 1211), in the Arthur Herbarium, sent by Rangel, which is labelled Panicum melinis. The specimen on Setaria is presumably no. 1212, therefore. This is confusing enough but Hitchcock believed the host of no. 1211 to be Digitaria sanguinalis (see Arthur, 5) and Arthur decided, with justification, that the rust was identical with the type of U. Panici-sanguinalis. Furthermore, the urediospores do not agree with those figured by Rangel as from Panicum melinis. No telia are present. Perhaps a mixture of hosts is the correct explanation for this confusing situation.

Under his description of U. niteroyensis Rangel (l.c.) notes "A U. Puttemansii praecique uredosporis diversa" and his illustrations show teliospores and paraphyses like those figured for P. Puttemansii and one smaller urediospore. The figure of the urediospore appears to be an end view. His measurements for the urediospores of U. niteroyensis (20–26 \times 24–28 μ) are smaller than he gives for U. Puttemansii (24–28 \times 24–40 μ). Dr. Thurston examined our type specimen in 1932 and his notes give the urediospores as 19–23 \times 24–27 μ , the measurements based upon four spores. I did not see urediospores in sections of the telia nor uredia on the rather fragmentary specimen.

Because of the apparent identity of the specimens examined with the figures published by Rangel I believe adoption of the name *U. Puttemansii* is justified.

U. Puttemansii differs from U. leptodermus in having teliospores with persistent pedicels, an apical wall noticeably thickened and larger urediospores. The large urediospores also separate it from P. catervaria but make confusion with P. Chaetochloae possible, except when telia are present. The uredia of P. Chaetochloae are longer covered, however, the ruptured epidermis is more conspicuously persistent as a cap, and the urediospores tend to be more angular.

Puccinia Chaetochloae Arth., Bull. Torrey Club 34: 585. 1907. (figs. 15, 16.)

(Uredo Chaetochloae Arth. Bull. Torrey Club 33: 518. 1906; Puccinia Maublancii Rangel, Arch. Mus. Nac. Rio de Janeiro 18: 159. 1916; Dicaeoma Chaetochloae Arth. & Fromme, N. Am. Flora 7: 288. 1920.)

Aecial stage unknown. Uredia amphigenous, scattered, oval or linear 0.5-2.0 mm. long, cinnamon-brown, the epidermis opening by a longitudinal slit or by circumcisal rupture, the epidermal cap then long persistent; paraphyses thin-walled, hyaline or yellowish, cylindric, inconspicuous; urediospores broadly ellipsoid, ellipsoid or oblong, commonly angular, variable in size, $(19-)22-27(-30) \times (26-)30-38(-43) \mu$; wall cinnamon-brown, 2μ thick, rather sparsely and strongly echinulate; pores 3 or 4, equatorial. Telia amphigenous, oblong or linear, 0.5-1.0 mm. long, blackish brown, remaining covered by the epidermis; teliospores irregular due to pressure in the compact, covered sorus, clavate, oblong or ellipsoid, rounded or somewhat obtuse above, usually narrowed below, slightly constricted at septum, (18-)20- $26 \times (29-)32-40(45) \mu$; wall chestnut-brown, 1.5 μ thick at sides, thickened at apex to 2-4 µ, smooth; pedicel, sometimes laterally placed, persistent, yellowish or golden-brown. Mesospores occasional.

MATERIAL EXAMINED: Paspalum arundinaceum Poir.: Dominican Republic: Ekman (Ciferri, Mycofl. Doming. Exs. 105). P. densum Poir.; Brazil: Rangel 1162 (type of P. Maublancii Rangel). P. floridanum Michx.; U. S. A.: Bartholomew (Barth., N. Am. Ured. 2776 as P. substriata); Lewis & Tharp; Long 2745, 2821. P. glabrum Poir.; Puerto Rico: Stevens 1732. P. millegrana Schrad.; Puerto Rico: Whetzel, Kern & Toro 2331; Whetzel & Olive 439. P. secans Hitchc. & Chase; Puerto Rico: Holway 20. Setaria geniculata Beauv.; Venezuela: Chardon, Toro & Alamo 163. S. macrosperma (Schribn. & Merr.) Schum.; U. S. A.: Bessey 41, 59; Holway (type).

Because of a paucity of telia it has been difficult to reach a decision concerning the morphological limitations, the hosts and the distribution of this species. Telia are present on *Setaria macrosperma* in three Florida specimens, including the type, on *P. densum* in the type of *Puccinia Maublancii* from Brazil and on *P. floridanum* from Oklahoma. The Oklahoma specimen was

issued as no. 2776 in Bartholomew, North American Uredinales as Puccinia substriata. In these specimens the telia are long covered, the spores are variable and angular, and their walls are rather brittle and easily crushed. The uredia also are tardily dehiscent, with the elevated epidermis usually conspicuous. While the species is probably less closely related to P. substriata than to P. dolosa, P. circumdata, and P. catervaria it is more apt to be confused with P. substriata, and Uromyces Puttemansii in the absence of telia, because of the large urediospores.

Microscopically and macroscopically the telia of *P. Chaetochloae* are similar to those of *P. circumdata*, *P. dolosa*, and *P. catervaria*. In size the teliospores are close to those of *P. dolosa* but larger than those of *P. catervaria* and *P. circumdata*. The urediospores, however, are larger, especially longer, have thicker walls, and approach those of *P. substriata*. It has been difficult with uredial collections to decide whether specimens should be referred to *P. Chaetochloae* or to *P. substriata*. It seems to be rather constantly true, however, that the urediospores of *P. Chaetochloae* are angularly ellipsoid or oblong-ellipsoid while those of *P. substriata* are broadly ellipsoid or obovoid and not angular. The pores in *P. substriata* tend to be slightly below the equator, which is not the case in *P. Chaetochloae*, and are usually four, less commonly three or five, in number.

Puccinia catervaria Cummins, sp. nov. (FIGS. 17, 18).

Urediis amphigenis, sparsis, paraphysibus periphericis dilute brunneis inconspicuis; urediosporae late ellipsoideae vel obovoideae, $19-24\times24-29~\mu$; membrana cinnamomeo-brunnea 1.5–2 μ cr., moderate echinulata; poris germ. 4, aequatorialibus. Teliis plerumque epiphyllis, sparsis, atrobrunneis, diutius tectis; teliosporae variabiles angulariter ellipsoideae, oblongo-ellipsoideae vel clavatae, $(18-)20-23\times26-33~\mu$; membrana $1-1.5~\mu$ cr., ad apicem $2-3.5~\mu$ cr., castaneo-brunnea, levi; pedicello sporam breviore, brunneolo, persistenti.

On Setaria geniculata in Bolivia.

Aecial stage unknown. Uredia amphigenous, scattered, elliptic, 0.2–0.7 mm. long, cinnamon-brown, with peripheral cylindric or clavate, thin-walled, pale brownish and rather inconspicuous paraphyses, the epidermis opening widely by longitudinal rupture; urediospores broadly ellipsoid or obovoid, 19– 24×24 – 29μ ; wall cinnamon-brown, moderately echinulate, 1.5– 2μ thick; pores 4, equatorial. Telia mainly epiphyllous, scattered, minute,

oblong, 0.1–0.3 mm. long, blackish brown, remaining covered by the epidermis; teliospores variable and usually angular due 20 pressure in the compact, covered sori, ellipsoid, oblong-ellipsoid or clavate, more or less rounded at each end, constricted at the septum, $(18-)20-23 \times 26-33 \,\mu$; wall chestnut-brown, $1-1.5 \,\mu$ thick at sides, thickened apically to $2-3.5 \,\mu$, smooth; pedicel, frequently lateral, shorter than the spore, brownish, persistent.

MATERIAL EXAMINED: Setaria geniculata (Lam.) Beauv.: Bo-LIVIA: Cochabamba, Feb. 28, 1920, Holway 348 (type) (Reliq. Holw. 53 as Puccinia levis).

This rust was included by Arthur (5) under *Puccinia levis*, a species with which it has no characters in common. The presence of telia was not recognized.

Morphologically, *P. catervaria* is related, perhaps too closely, to *P. circumdata* which appears, however, to be restricted to *Panicum fasciculatum*. In addition to the apparent host restriction, *P. catervaria* has urediospores with four pores and the spores lack the triangular shape of those of *P. circumdata*. It seems best, without knowledge of the aecial stages, to maintain *P. circumdata* and *P. catervaria* as separate species.

Puccinia circumdata Mains, Carnegie Inst. Washington Publ. 461: 101. 1935. (Fig. 13.)

Aecial stage unknown. Uredia amphigenous, scattered, elliptic or oblong-linear, 0.3-0.8 mm. long, cinnamon-brown, the epidermis ruptured by a longitudinal slit; hyaline or brownish, clavate or cylindric, thin-walled paraphyses present but not conspicuous; urediospores ellipsoid or obovoid, triangular in end view, $19-24 \times 23-32 \mu$; wall $1-1.5 \mu$, light cinnamon- or goldenbrown, finely echinulate; pores 3, equatorial, in the angles. Telia amphigenous, oval or oblong, 0.2-0.4 mm. long, blackish brown, remaining covered by the epidermis; teliospores irregular due to pressure in the compact, covered sori, oblong, oblong-ellipsoid, oblong-clavate or ellipsoid, usually angular, slightly constricted at septum, $17-24(-26) \times 26-33(-36) \mu$; wall brittle and easily crushed, $1-1.5 \mu$ thick at sides, slightly thickened at apex to $2-3 \mu$, chestnut-brown, smooth; pedicel about one-half length of spore or less, hyaline, sometimes laterally attached. Mesospores few or, in some collections, abundant.

MATERIAL EXAMINED: Panicum fasciculatum Sw.: Cuba: Johnston 641; MEXICO: Swallen 2389, 2592 (type); PANAMA:

Carleton 129; Johnston 2562; Killip 4148; Puerto Rico: Seaver & Chardon 2057; Stevens 7816; Whetzel & Olive 445.

Although first described by Mains this species was previously reported under other names. Arthur reported it in 1916 (2), 1917 (3) and 1918 (8) as P. Huberi. The records were reported similarly in 1920 by Arthur and Fromme (6, p. 287). In 1926 Arthur (6, p. 774) reduced P. Huberi to synonymy under P. levis. All collections were on P. fasciculatum. Mains (l.c.) reported Paspalum yucatanum as a host but I consider it to be P. dolosa.

No other rust on *Panicum* can well be confused with *P. circumdata*. *P. catervaria* is closely related but it parasitizes *Setaria* and has urediospores with four pores. *P. dolosa*, on *Paspalum*, has similar telia and similarly delicate and brittle, but larger teliospores. The urediospores also are triangular in end-view and have three pores but are smaller. Mains (*l.c.*) enumerated the differences between *P. circumdata* and *P. Chaetochloae*.

Puccinia dolosa Arth. & Fromme, Torreya 15: 262. 1915. (fig. 12.)

Aecial stage unknown. Uredia amphigenous or often mainly epiphyllous, evenly scattered, elliptic, 0.2-0.4 mm. long, pale cinnamon-brown, the epidermis rupturing by a longitudinal slit: paraphyses mainly peripheral, hyphoid or cylindric, hyaline or pale yellowish, inconspicuous; urediospores usually obovoid, triangular in end view, $16-20(-24) \times 19-25(-29) \mu$; wall $1-1.5 \mu$ thick, light cinnamon- or golden-brown, finely echinulate; pores 3, equatorial, in the angles. Telia amphigenous or mainly epiphyllous, scattered, oval or elliptic, 0.1-0.5 mm. long, blackish brown, remaining covered by the epidermis; teliospores variable due to pressure in the compact, covered sori, oblong, oblongclavate or clavate, usually angular, broadly rounded or obtuse above, usually narrowed below, slightly constricted at septum, $17-23(-26) \times 28-40(-45) \mu$; wall brittle and easily crushed, 1-1.5 \mu thick at sides, thickened to 2-4 \mu at apex, chestnutbrown, smooth; pedicel one-half as long as spore or less, yellowish or hyaline, sometimes laterally placed. Mesospores rare.

MATERIAL EXAMINED: Paspalum mandiocanum Trin.: BRAZIL: Holway 1675. P. multiflorum Doell.; BRAZIL: Holway 1478, 1642. P. paniculatum L.; BRAZIL: Holway 1464, 1469 (Reliq. Holw. 116, 117 as P. substriata), 1597, 1612 (Reliq. Holw. 131

as P. substriata), 1650, 1664, 1731, 1773, 1781, 1793; VENEZUELA: Barrus & Müller 3629: Chardon 1120: Müller 2028, 2084: Costa RICA: Stevens 425; MEXICO: Hitchcock 6874; Holway 3514; PANAMA: Carleton 232; PUERTO RICO: Thomas; Whetzel & Olive 391, 392. P. plicatulum Michx.: BRAZIL: Holway 1321 (Relig. Holw. 114 as P. substriata), 1504, 1647, 1659 (Relig. Holw. 136 as P. tubulosa); PUERTO RICO: Whetzel, Kern & Toro 2333. P. Regnelli Mez.; Brazil: Holway 1554 (Relig. Holw. 124 as P. substriata), 1602, 1643 (Reliq. Holw. 126, 133 as P. substriata), 1651, 1662, 1685 (Relig. Holw, 139 as P. substriata), 1696. P. tenellum Willd.; MEXICO: Holway (type) (Syd. Ured. 1986), 3065. P. Usteri Hack.: BRAZIL: Holway 1553 (Relig. Holw. 123 as P. tubulosa). P. virgatum L.; Brazil: Holway 1628 (Reliq. Holw. 132 as P. substriata); CUBA: Johnston 307. P. sp.; Brazil: Holway 1280 (Relig. Holw, 112 as P. substriata), 1697: GUATEMALA: Johnston 1696.

P. dolosa was published in 1915 by Arthur and Fromme (l.c.) but reduced to synonymy under P. Huberi in 1920 (6, p. 287). In 1925, Arthur (5) reduced P. Huberi to synonymy under P. levis and removed P. dolosa to the synonymy of P. substriata. Other than in these records P. dolosa seems to have been neglected.

The long-covered, small telia serve to separate *P. dolosa* from *P. Huberi*, *P. Puttemansii*, *P. substriata*, *P. araguata*, and *P. levis*. The telia can be easily overlooked but were found in two-thirds of the specimens. Failure to recognize the telia has probably been due in part to their subepidermal position and small size and in part to the brittle nature of the walls of the teliospores. In mounts made by scraping or crushing the teliospores are apt to be fragmented beyond recognition.

The character of brittleness is possessed in a like degree by the teliospores of *P. circumdata* and *P. catervaria* and to a lesser degree by those of *P. Chaetochloae*. *P. dolosa* is separable from *P. Chaetochloae* because of the small, thin-walled urediospores and from *P. catervaria* because of smaller, 3-pored urediospores and larger teliospores. The urediospores of *P. circumdata* likewise are angular and have three pores but are larger, while the teliospores are smaller.

SPECIES WITH EARLY-EXPOSED, PULVINATE TELIA

Puccinia substriata Ellis & Barth. Erythea 5: 47. 1897. (Figs. 4-6.)

(Dicaeoma substriatum Arth., Résult. Sci. Congr. Bot. Vienne 344. 1916; Puccinia Pilgeriana P. Henn. Bot. Jahrb. 40: 226. 1908; Uredo cubangoensis Rangel, Arch. Mus. Nac. Rio de Janeiro 18: 160. 1916; Puccinia tubulosa Arth. Am. Jour. Bot. 5: 464. 1918, in part; Dicaeoma tubulosum Arth. & Fromme, N. Am. Flora 7: 288. 1920, in part.)

AECIAL STAGE: Aecidium tubulosum Pat. & Gaill.; cultures made by Thomas (17). Uredia amphigenous or mainly hypophyllous, scattered, elliptic, 0.3-0.8 mm. long, cinnamon-brown, the epidermis opening broadly by longitudinal or irregular rupture; urediospores broadly ellipsoid or obovoid, (20-)23-30 X (25-)28-36 \mu; wall connamon-brown, 1.5-2 \mu thick with a tendency to be slightly thicker above, moderately echinulate; pores usually 4, less commonly 3 and rarely 5, equatorial or slightly below. Telia amphigenous or mainly hypophyllous, scattered, early naked, pulvinate, chestnut-brown or blackish brown, round, oval or oblong, 0.3-0.8 mm. long; teliospores oblong-ellipsoid or clavate, rounded or somewhat obtuse above, narrowed below, slightly constricted at septum, $19-26(-29) \times (29-)33-50 \mu$; wall chestnut-brown or frequently golden-brown in tropical collections, $1.5-2 \mu$ thick at sides, $3-7 \mu$ at apex, smooth; pedicel about one-half as long as spore, hyaline or yellowish, persistent. Mesospores and 3-celled spores rarely present.

MATERIAL EXAMINED: Paspalum affine Steud.: GUATEMALA: Standley 63781. P. Bushii Nash; U. S. A.: Learn. P. ciliatifolium Michx.; U. S. A.: Arthur; Holway; Lewis & Tharp. P. conjugatum Berg.; Puerto Rico: Stevens 9237. P. Curtisianum Steud.; U. S. A.: Hitchcock 500. P. denticulatum Trin.; U. S. A.: Arthur & Fromme 6308. P. distichophyllum H.B.K.; Brazil: Holway 1640, 1672. P. distichum L.; Peru: Holway 781 (Reliq. Holw. 94). P. Hankeanum Presl; Peru: Holway 786. P. Humboldtianum Fluegge; Bolivia: Holway 678, 712; Peru: Holway 782. P. langei (Fourn.) Nash; Guatemala: Standley 90063; U. S. A.: Clover 1656; Venezuela: Sydow (Fung. Exot. Exs. 775 as P. paspali). P. malacophyllum Trin.; Brazil: Holway 1645 (Reliq. Holw. 135 as P. tubulosa), 1646, 1725, 1873. P. mandiocanum Trin.; Brazil: Holway 1677, 1690,

Rangel 1143 (type of Uredo cubangoensis Rangel). P. molle Poir.: VENEZUELA: Chardon & Toro 509, Müller 2331. P. paniculatum L.; Bolivia: Holway 726; Brazil: Holway 1568 (Relig. Holw. 125 as P. tubulosa), 1630, 1679; Costa Rica: Bethel: DOMINICAN REPUBLIC: Ekman (Ciferri, Mycofl. Doming. Exs. 74 as P. tubulosa); GUATEMALA: Holway 595; PUERTO RICO: Stevens 293, 898, 4758, 7313, 8048, 8444, 8645; Stevenson 3995; Thomas 3 coll.; Whetzel, Kern & Toro 2324, 2335; Whetzel & Olive 393, 411; VENEZUELA: Chardon & Toro 503. P. pilosum Lam.; Brazil: Holway 1948. P. plantagineum Nees; Brazil: Holway 1937. P. pruinosum Trin.; BRAZIL: Holway 1482, 1644 (Relig. Holw. 134 as P. tubulosa). P. pubescens Muhl.; U. S. A.: Cummins. P. remotum Remy; Bolivia: Holway 336 (Relig. Holw. 51). P. setaceum Michx.: U. S. A.: Bartholomew (type) (E. & E. N. Am. Fungi 3577; Fungi Columb. 1186), (Svd., Ured. 1080), (Barth., N. Am. Ured. 2167), 7023; Bates 3052. P. stramineum Nash; U. S. A.: Bates (Barth., Fungi Columb. 4673). P. trachycauleon Steud.; VENEZUELA: Barrus 3738; Tamayo 3767; Whetzel & Müller 2845. P. Usteri Hack.; BRAZIL: Holway 1641, 1676. P. virgatum L.; PUERTO RICO: Whetzel, Kern & Toro 2330. P. sp.; Brazil: Holway 1727; Pilger (type of P. Pilgeriana); British Honduras: Mains 3799, 3863; Peru: Abbott; U. S. A.: Long 2740. Setaria lutescens (Weigel) F. T. Hubb.; U. S. A.: Clover 961. Valota saccharata (Buckl.) Chase; BOLIVIA: Holway 321, 368 (Reliq. Holw. 60 as P. tubulosa); CUBA: Johnston 1040; GUATEMALA: Holway 857; Kellerman 5368; PUERTO RICO: Whetzel, Kern & Toro 2122, 2127, 2308, 2346, 2347; Whetzel & Olive 394, 436, 447.

P. substriata is the only species in this paper whose aecial stage (Aecidium tubulosum) has been indicated by collectors and also proved by cultures. Field observations made by Whetzel and Olive (13) led them to believe that this Aecidium on Solanum was the alternate stage of P. substriata on Paspalum and their germination experiments proved it to be a true Aecidium. They credit Stevenson with having reached a similar conclusion. Holway observed close association between A. tubulosum and rusted Paspalum. Arthur (5) recorded these observations under P. tubulosa, since he (4) had previously concluded that the

species was distinct from P. substriata. In 1918, working in Puerto Rico, Thomas (17) proved the life cycle by experimental methods and reported his results as applying to P. substriata. Arthur (7) reported, under P. paspalicola, aecia on Solanum elaeagnifolium in Texas and on S. carolinense in Iowa. On Oct. 15, 1941, I obtained uredia and telia of P. substriata on Paspalum pubescens near Oaktown, in southern Indiana. This material was overwintered at Lafayette and plants of S. carolinense, grown from seed, were inoculated on May 5, 9 and 12, 1942. Pycnia developed May 19 followed by aecia June 1. The spores from these aecia measured $18-23 \times 23-29 \,\mu$ and thus fall in the lower range of measurements for the tropical aecia on Solanum. This culture demonstrates that P. substriata, as it occurs on Paspalum, in the United States, forms aecia on the genus Solanum as it does in the tropical regions.

Because of the availability of the type of *Uredo paspalicola* and the widespread presence of similar uredia on tropical species of *Paspalum*, often in association with uredia and telia of *P. substriata*, Arthur (4) and Arthur and Fromme (6, p. 288) published *U. paspalicola* as a synonym under the name, *P. tubulosa*. Arthur (4) made the new combination although Arthur and Fromme appear as co-authors in the Flora where they also recognized *P. substriata*, without synonyms, as a species. Later, Arthur (6, p. 774) added *P. Pilgeriana* P. Henn. to the synonymy of *P. tubulosa* and cited nine synonyms under *P. substriata*. The situation remained static until 1934 when Arthur (7) placed *P. tubulosa* under the new combination, *P. paspalicola* (P. Henn.) Arth.

In 1934, Mains (12) described the genus Angiopsora and included, by transfer, Puccinia compressa Arth. & Holw. Apparently Arthur did not recognize the similarity between Uredo paspalicola and the uredia of P. compressa when he (5) described P. compressa. This seems strange since he recorded uredial collections along with the type, but assigned identical uredial collections (Holway 1607, 1633) as well as collections (Holway 719; Reliq. Holw. 87) with telia to P. tubulosa (l.c., p. 174). Moreover, he assigned both uredial collections (Holway 1418, 1476) and telial collections (Holway 703) to P. substriata (l.c.,

p. 171, 172). Uredo paspalicola is synonymous with Angiopsora compressa and P. tubulosa becomes synonymous with P. substriata. Cummins (9) has published the synonymy, hosts and distribution of A. compressa.

Because of erumpent, compact telia *P. substriata* differs from *P. Chaetochloae* and *P. dolosa*. In so far as telia are concerned *P. substriata* has a general similarity to *P. araguata* but the teliospores of *P. araguata* are larger, especially broader, and the urediospores are thinner-walled and paler in color.

As recorded above, the urediospores of P. substriata tend to have the wall slightly thickened apically. This varies but is commoner in tropical collections. The apical thickening is not evident in the type but in a Venezuelan collection (Tamayo 3767) it is much exaggerated (FIG. 9) and accompanied by increased lateral wall thickness. I am inclined to believe that the latter collection is an amphisporic variant of P. substriata. The tendency of the germ pores to be slightly subequatorial is evident in the type, in most collections showing the apical thickening, and in the amphisporic form, but is not constant. The pores are strictly equatorial in some collections, as those on Valota. Some variation exists also in the number of pores, but they are usually four. In general those spores which show a tendency to be thickened apically also tend to be slightly larger. The teliospores in tropical collections, except on Valota, tend to be shorter than in the type.

These tendencies and variations are not sufficiently striking to justify further segregation. They can be evaluated with accuracy only after the species has been studied by cultural methods.

Puccinia araguata Kern, Mycologia 30: 544. 1938. (Fig. 10.) (Puccinia paspalicola Kern, Thurston & Whetzel, Monogr. Univ. P. Rico B. 2: 284. 1934 (Oct.). Not P. paspalicola Arth. 1934 (June).

Aecial stage unknown. Uredia amphigenous, scattered, elliptic or linear, 0.5–1 mm. long, the epidermis rupturing longitudinally and remaining rather conspicuous, pale cinnamon- or golden-brown; urediospores obovoid or ellipsoid, $19-23(-25) \times 27-35 \mu$; wall pale golden or yellowish, $1-1.5 \mu$ thick, finely

echinulate; pores obscure, equatorial, 4 where seen with certainty. Telia epiphyllous, scattered, oval or linear, 0.3–0.8 mm. long, blackish brown, pulvinate, surrounded by the upturned epidermis; teliospores broadly clavate or oblong-clavate, broadly rounded above, somewhat narrowed below, only slightly constricted at septum, (20–)24–30 \times (40–)44–53(–63) μ ; wall dark cinnamon- or light chestnut-brown, 1.5–2.5 μ thick at sides, thickened apically to 4–9 μ , smooth; pedicel broad, shorter than spore and usually broken at or near hilum.

MATERIAL EXAMINED: Paspalum microstachyum Presl: VENEZUELA: Chardon & Toro 600 (type).

P. araguata is a distinctive species with more the macroscopic appearance of P. macra Arth. & Holw. than of P. substriata. The teliospores are broader than those of P. substriata and of different shape than those of P. macra. The urediospores are paler than those of P. substriata and are distinct from the similarly colored spores of P. macra because of the equatorial pores.

Puccinia macra Arth. & Holw.; Arth. Am. Jour. Bot. 5: 465. 1918. (fig. 23.)

(Dicaeoma macrum Arth. & Fromme, N. Am. Flora 7: 287. 1920.)

Aecial stage unknown. Uredia mainly hypophyllous, oval or linear, 0.5–1 mm. long, scattered or in linear groups, orange or yellowish, the epidermis opening by longitudinal rupture and remaining more or less conspicuous; urediospores ellipsoid or broadly ellipsoid, $23-29 \times 28-35 \,\mu$; wall $1-1.5 \,\mu$ thick, yellowish, finely and rather sparsely echinulate; pores about 8, scattered, obscure. Telia hypophyllous and on sheaths, oval or oblong, 0.5–1.5 mm. long, scattered or in groups, early naked, pulvinate, blackish brown, sometimes with few brownish, hyphoid paraphyses; teliospores clavate, oblong-clavate or less commonly ellipsoid, rounded or rarely nearly truncate above, narrowed or rarely rounded below, slightly constricted at septum, $20-28 \times (35-)39-50(-56) \,\mu$; wall chestnut-brown or somewhat paler, $2 \,\mu$ thick at sides, $5-8 \,\mu$ at apex, smooth; pedicel about as long as spore, golden, moderately thin-walled, persistent.

MATERIAL EXAMINED: Paspalum candidum (Humb. & Bonpl.) Kunth: Bolivia: Holway 697; Costa Rica: Sydow 292; Guatemala: Holway 168 (type); Venezuela: Barrus & Müller 3625. P. prostratum Scribn. & Merr.; Colombia: Chardon 816.

P. macra is distinctive because of the pale uredia, yellowish thin-walled urediospores with scattered pores and the large clavate teliospores. The species was recorded from Ecuador by Arthur (5) but the specimens have thick-walled, verrucose urediospores and are cited under P. pseudoatra.

Puccinia pseudoatra Cummins, sp. nov. (FIG. 21).

Urediis amphigenis, seriatim dispositis vel sparsis, dilute cinnamomeobrunneis; urediosporae globoideae, $22-26 \times 23-27 \mu$; membrana aureo- vel pallide cinnamomeo-brunnea, $2.5-3 \mu$ cr., verrucosa; poris germ. 7 vel 8, sparsis. Teliis urediis conformibus sed atro-brunneis, pulvinatis; teliosporae ellipsoideae, $21-26 \times 29-37 \mu$; membrana castaneo-brunnea, $2-3 \mu$ cr., ad apicem $5-8 \mu$; pedicello flavidulo, persistenti, sporam aequantae vel longiore.

On Paspalum pallidum, P. penicillatum, P. prostratum in Bolivia and Ecuador.

Aecial stage unknown. Uredia amphigenous or sometimes only hypophyllous, in linear groups or scattered, oval or linear, 0.3–1.5 mm. long or longer by confluence, light cinnamon-brown, the epidermis rupturing longitudinally and remaining conspicuous; urediospores globoid, less often broadly ellipsoid, $22-26 \times 23-27 \mu$; wall golden- or light cinnamon-brown, closely and finely verrucose, the beads uniting in irregular, labyrinthiform lines, $2.5-3 \mu$ thick; pores 7 or 8 scattered. Telia like the uredia but blackish brown and pulvinate; teliospores ellipsoid, rounded at both ends or slightly narrowed below, only slightly constricted at septum, $21-26 \times 29-37 \mu$; wall $2-3 \mu$ thick at sides, $5-8 \mu$ at apex, deep chestnut-brown, smooth; pedicel persistent, pale yellowish, relatively thin-walled, one or two times as long as spore.

On Paspalum pallidum H.B.K.: ECUADOR: Quito, Aug. 17, Aug. 30, 1920, Holway 909, 954 (type) (Reliq. Holw. 100 as P. macra). Paspalum aff. pallidum; ECUADOR: Ambato, 1920, Pachano 106, 108. P. penicillatum Hook.; ECUADOR: Quito, May 1890, Lagerheim. P. prostratum Scribn. & Merr.; BOLIVIA: Sorata, Apr. 12, 1920, Holway 507 (Reliq. Holw. 79 as P. atra).

The above specimens were reported by Arthur (5) variously as P. panicophila, P. macra and P. atra.

P. pseudoatra has nothing in common with P. macra. The urediospores agree with those of P. Setariae in type of sculpture and arrangement of pores but are smaller, as are the teliospores. The teliospores have the shape of those of P. atra but are smaller,

while the urediospores are smaller and have scattered pores. A somewhat similar rust on *Valota insularis* is discussed under *P. atra*.

Puccinia atra Diet. & Holw.; Holway, Bot. Gaz. 24: 29. 1897. (Figs. 19, 20, 22.)

(Puccinia eslavensis Diet. & Holw.; Holway, Bot. Gaz. 24: 29. 1897; Dicaeoma atrum Arth. Résult. Sci. Congr. Bot. Vienne 344. 1906; Dicaeoma eslavensis Arth. Résult. Sci. Congr. Bot. Vienne 344. 1906; Puccinia panicophila Speg. Anal. Mus. Nac. Buenos Aires 19: 300. 1909.)

Aecial stage unknown. Uredia amphigenous or mainly hypophyllous, scattered or usually in linear groups, oval or linear, 0.5–1 mm. long or longer by confluence, cinnamon-brown, the epidermis rupturing, longitudinally and remaining more or less conspicuous; urediospores globoid, broadly ellipsoid, ellipsoid or obovoid, $(22-)24-29 \times (25-)27-32(-35) \mu$; wall cinnamon- or golden-brown, 2.5–3.5 μ thick, closely and finely verrucose, the beads more or less united in irregular labyrinthiform lines; pores 4–6, equatorial or somewhat scattered in occasional spores. Telia like the uredia but blackish-brown and pulvinate; teliospores ellipsoid, rounded at both ends or slightly narrowed below, slightly or not constricted at septum, $22-29 \times 30-41 \mu$; wall deep chestnut-brown, smooth, 2.5–3.5 μ thick at sides, 4–8 μ at apex; pedicel one and one-half or two times as long as spore, persistent, yellowish, thick-walled.

MATERIAL EXAMINED: Leptoloma cognatum (Schultes) Chase: U. S. A.: Clemens. Panicum bulbosum H.B.K.; MEXICO: Hitchcock; Holway (type of P. eslavensis D. & H.), 3140; Pringle 6418, P. bulbosum sciaphilum (Rupr.) Hitchc. & Chase; MEXICO: Hitchcock; U. S. A.: Holway (Syd., Ured. 1308); Long 5278a; Wilcox. Paspalum Helleri Nash; PUERTO RICO: Stevens 8999. P. sp.; ECUADOR: Holway 824a. Pennisetum bambusiforme Hemsl.; MEXICO: Pringle 6075. P. chilense (Desv.) Jacks.; BOLIVIA: Holway 438 (Reliq. Holw. 70), 605. Setaria Grisebachii Four.; MEXICO: Holway (type), 3040, 3153, 3165, 3521. Valota insularis (L.) Chase; BRAZIL: Holway 1082, 1152, 1290 (Reliq. Holw. 113), 1704; GUATEMALA: Holway 205; Kellerman 5469; MEXICO: Holway 3638; PUERTO RICO: Seaver 825; Whetzel, Kern & Toro 2250, 2260. V. saccharata (Buckl.) Chase;

ARGENTINA: Spegazzini (type of *P. panicophila* Speg.); MEXICO: Hitchcock 5615; U. S. A.: Arthur & Fromme 5607, Clemens.

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The collections have similar teliospores, varying only slightly in size and not at all in shape, but the urediospores are less constant. The form on *Panicum bulbosum*, originally segregated as *P. eslavensis*, tends to have somewhat longer, more ellipsoid

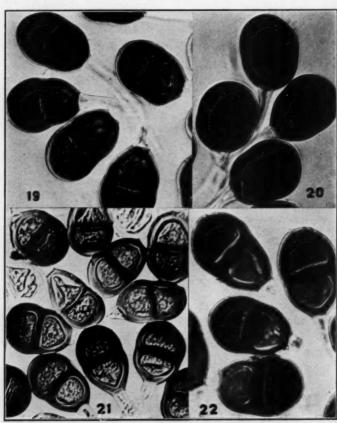


Fig. 19, teliospores of Puccinia atra D. & H. on Setaria grisebachii (from type); 20, teliospores of Puccinia eslavensis D. & H. (=P. atra) on Panicum bulbosum (from type); 21, teliospores of Puccinia pseudoatra Cumm. on Paspalum pallidum (from type); 22, teliospores of Puccinia panicophila Speg. (=P. atra) on Valota saccharata (from type). \times 700.

urediospores than the type of *P. atra*. This is also true of the rust on *Pennisetum chilense* which, however, has three or four pores while the type of *P. eslavensis* usually has five or six. The collection on *Pennisetum bambusiforme* is more like the type of *P. atra*. There appears to be no reason for retaining *P. panicophila* on *Valota saccharata* as a species. North American material on the same host differs in no way.

However, the rust on *Valota insularis* is more troublesome. North American collections have urediospores with four equatorial pores or with four in the equator and one near the apex while South American collections have the pores commonly scattered and five to seven or less often equatorial and four or five. In both the spores are usually under $30~\mu$ in length. The arrangement of pores is in part that of *P. atra* and in part that of *P. pseudoatra*. The North American rust appears to be nearer *P. atra* while the South American rust is perhaps nearer *P. pseudoatra*. Nevertheless, I am placing them together under *P. atra*, although this may not be correct.

In his report on the Holways' South American collections Arthur (5) reported *P. atra* on *Paspalum prostratum* from Bolivia. This I consider to be *P. pseudoatra*.

Puccinia Setariae Arth. & Holw.; Holway, Bot. Gaz. 24: 28. 1897. (fig. 24.)

(Dicaeoma Setariae Arth. Résult. Sci. Congr. Bot. Vienne 344. 1906.)

Aecial stage unknown. Uredia amphigenous or mainly hypophyllous, scattered or in linear groups, 0.5–2 mm. long, cinnamonbrown, the epidermis rupturing widely and remaining more or less conspicuous; urediospores globoid, broadly ellipsoid or less commonly ellipsoid or obovoid, $(23-)25-29\times(27-)29-34\,\mu$; wall light cinnamon- or golden-brown, 2.5–3.5 μ thick, finely and closely verrucose, the beads usually united in irregular, labyrinthiform lines; pores 7 or 8, scattered, usually evident. Telia like the uredia but blackish brown and pulvinate; teliospores elllipsoid, rounded at both ends or slightly narrowed at base, slightly or not constricted at septum, $24-32\times37-48\,\mu$; wall chestnut-brown, smooth, $3-5\,\mu$ thick at sides, $8-11\,\mu$ at apex; pedicel persistent, yellowish or hyaline, moderately thick-walled, about twice as long as spore.

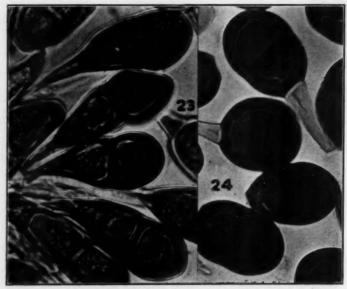


Fig. 23, teliospores of *Puccinia macra* Arth. & Holw. on *Paspalum candidum* (from type); 24, teliospores of *Puccinia Setariae* Diet. & Holw. on *Setaria geniculata* (from type). × 700.

MATERIAL EXAMINED: Setaria geniculata (Lam.) Beauv.: ARGENTINA: Holway 2028; CHILE: Holway 290; GUATEMALA: Johnston 1699; MEXICO: Holway (type), 3126, 3156, 3556; U. S. A.: Edgerton 719.

Puccinia Setariae is macroscopically like P. atra and P. pseudoatra but differs from both in having larger teliospores, from P. atra because of consistently scattered pores, and from P. pseudoatra because of larger urediospores. The three species probably are closely related.

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PUCCINIA HUBERI P. Henn., Hedwigia Beibl. 39: 76. 1900. (FIG. 11.)

(Dicaeoma Huberi Arth. & Fromme, N. Am. Flora 7: 287. 1920.)

Aecial stage unknown. Uredia amphigenous, scattered in elongate brown spots, elliptic, 0.2-0.4 mm. long, pale cinnamon-brown, the epidermis rupturing by a longitudinal slit; uredio-

spores ellipsoid, broadly ellipsoid or obovoid, $18-23 \times 20-27~\mu$; wall $1.5~\mu$ thick, pale cinnamon-brown or yellowish, rather finely and sparsely echinulate; pores equatorial, 3 or 4. Telia on spots like the uredia, round or oval, 0.2-0.5~mm. long, pulvinate, chestnut-brown, the longitudinally or irregularly ruptured epidermis conspicuous; teliospores variable in size and shape, ellipsoid or clavate, frequently diorchidioid, rounded above and below or usually narrowed below, slightly constricted at septum, $18-26 \times 24-39~\mu$; wall $2~\mu$ thick at sides, thickened to $2.5-5~\mu$ at apex but without a distinctly paler umbo, smooth; pedicel, frequently lateral, persistent, golden-brown, about one-half as long as spore. Mesospores numerous.

MATERIAL EXAMINED: Panicum ovalifolium Poir.: BRAZIL: Huber 3 (type). P. trichoides Sw.; PUERTO RICO: Clinton 119; Seaver & Chardon 1517; Stevens 82, 194, 4973, 5981, 7815, 8280, 8472, 8974; Stevenson 5029; Whetzel, Kern & Toro 2258, 2322; Whetzel & Olive 414, 415, 416, 433; VENEZUELA: Sydow (Syd., Fungi Exot. Exs. 771).

P. Huberi differs from the other rusts on Panicum in producing conspicuous, more or less striately arranged, brown, necrotic spots around the sori. The erumpent, pulvinate telia also distinguish it from P. circumdata while the small, mainly clavate or ellipsoid teliospores and pale urediospores are different from those of P. levis. P. Puttemansii is similar in the erumpent telia and the size and shape of its spores but the teliospores are paler, the apical wall is thicker, the thickening being in the nature of a paler differentiated umbo, and the lateral walls are thinner.

P. Huberi has been variously treated. Arthur (1, 3) accorded it specific rank adding, in the latter report, P. Puttemansii as a synonym. Arthur & Fromme (6, p. 287) treated it similarly but added as a synonym, P. dolosa. Then Arthur (5) removed P. dolosa to the synonymy of P. substriata and reduced P. Huberi and P. Puttemansii to synonymy under P. levis. Sydow (14) and Kern, Thurston and Whetzel (11) retain P. Huberi as a species.

PUCCINIA PUTTEMANSII P. Henn. Hedwigia 41: 105, 1902. (FIG. 14.)

Aecial stage unknown. Uredia scattered, amphigenous or mainly hypophyllous, oval or linear, 0.1×0.2 -0.6 mm., pale

cinnamon-brown, pulverulent, the epidermis opening by a longitudinal slit; urediospores obovoid or broadly ellipsoid, 19–24 \times 25–31 μ ; wall yellowish or pale golden-brown, 1.5 μ thick, moderately echinulate; pores equatorial, 4 or less commonly 3. Telia scattered, mainly hypophyllous, round or ellipsoid, 0.1–0.3 \times 0.2–0.8 mm., early naked, pulvinate, chestnut-brown, the surrounding ruptured epidermis conspicuous; teliospores clavate, oblong-clavate or oblong-ellipsoid, rounded or somewhat obtuse above, narrowed below, only slightly constricted at septum, 16–20 \times (27–)30–37(–40) μ ; wall light chestnut- or golden-brown, 1.5 μ thick at sides, apex thickened to 4–7 μ by a paler umbo, smooth; pedicel persistent, yellowish, equal to or less than length of spore. Mesospores occasional.

MATERIAL EXAMINED: Panicum millegrana Poir.: BRAZIL: Holway 1575, 1619, 1717 (Reliq. Holw. 140 as P. levis), 1850a, 1852a, 1921a, 1924. P. sciurotis Trin.; BRAZIL: Holway 1824 (Reliq. Holw. 143 as P. tubulosa). P. sp.; BRAZIL: Puttemans 140 (type).

P. Puttemansii was placed under P. Huberi by Arthur and Fromme (6, p. 287) but removed by Arthur (5) to the synonymy of P. levis. In this later report the Holway specimens listed above were included under P. levis and P. tubulosa. The "a" numbers were segregated from collections in which both rusts occurred in close association. This mixture was apparently obvious in the field since Holway noted in no. 1850 that two Uredos were present, one brown and one yellow and again in no. 1921: "with oblong, yellow-brown III." These differences are more or less obvious in dry material and, coupled with microscopic differences, make the two species easy to distinguish.

P. Puttemansii differs from P. Huberi in lacking brown necrotic spots. The teliospores are somewhat paler, have thinner side walls and thicker apex, the latter being pale and conspicuous as a more or less differentiated umbo.

As published by Arthur (5) the host of no. 1852 (see no. 1852a above) was listed as Cymbopogon rufus, but it is obviously a Panicum and apparently P. millegrana.

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TAXONOMIC NOTES ON MYXOMYCETES

G. W. MARTIN

(WITH 3 FIGURES)

CALONEMA AUREUM Morgan.

Lister (Mycetozoa ed. 3: 217. 1935) says of this species: "It is closely allied to Oligonema flavidum, of which it appears to be hardly more than a variety." Hagelstein (Mycologia 31: 341. 1939; 32: 377. 1940) notes its resemblance to A. nitens. from which it differs in its more golden color and the netted capillitium, in addition to the characteristic markings of the latter. Careful examination of a large number of collections of both O. flavidum and O. nitens and of a smaller but adequate number of collections of Calonema aureum failed to disclose any that I should regard as intermediate. In addition to the constant presence of a capillitial net, and the characteristic capillitial markings of the Calonema, both capillitium and sporangium wall turn a bright pinkish orange when a weak solution of potassium hydroxide is added to a mount, whereas the only effect of this solution on any Oligonema is to cause a slight intensification of the yellow-brown color of the sporangium wall.

CERATIOMYXA FRUTICULOSA (Muell.) Macbr.

Attempts have been made to distinguish species of *Ceratiomyxa* on the basis of the color of the plasmodium. On June 11, 1934, following heavy rains, *C. fruticulosa* was observed fruiting abundantly on fallen aspens in a ravine a few miles north of Iowa City. On some logs the plasmodia were colorless upon emergence, becoming milky and producing white fructifications. In about an equal number of cases the plasmodia were a brilliant yellowgreen and produced greenish-yellow fructifications. The two forms were usually on separate logs, but in one instance both were emerging from the same log in close proximity to each other, although apparently not in contact. Two portions of

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wood bearing plasmodia, one white and one green, were brought into the laboratory and placed in a moist chamber, with the hope that the plasmodia might be made to mingle, and perhaps fuse. This did not occur, as both proceeded to fructification, the fruitings in both cases being white and indistinguishable from each other. The yellow fruitings collected in the field, when dried in the laboratory, faded to pale ochraceous. This observation, while far from conclusive, is another suggestion that too great emphasis should not be placed on color, either of plasmodium or of fructification, in the myxomycetes.

CERATIOMYXA SPHAEROSPERMA Boedijn.

This minute species, originally described from Sumatra (Misc. Zool. Sumatrana 24: 1. 1927), has recently been reported from the island of Krakatoa (Boedijn, Bull. Jard. Bot. Buitenzorg III.

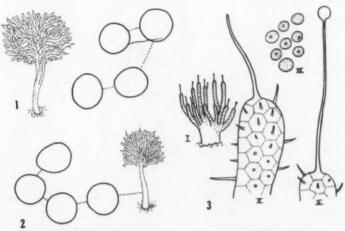


Fig. 1, Ceratiomyxa sphaerosperma, from Costa Rica, fructification, × 20, spores, × 1000; 2, same, from Panama, same magnifications; 3, same, tracing of Boedijn's illustrations, reduced to 5/12 original size.

16: 361. 1940). Its distinctive characters are the very small, scattered fructifications, each consisting of a single stalk bearing a head of several to many nearly equal, scarcely forking branches, the rather small globose spores and the tendency for some of the

spores, particularly those borne at the tips of the branches, to be produced on exceptionally long, slender stalks. I have two collections. One (G.W.M. 4098) was collected by M. L. Shields on Barro Colorado Island, Panamá Canal Zone, August 11, 1937, on dead fruits of Apeiba tibourbou Aubl. and I have been holding it as a probable new species, since Boedijn's original description. published in a zoological journal of limited circulation, had escaped my notice until recently. When an additional specimen, collected by Dr. C. W. Dodge on dead wood at Castilla, Limon Province, Costa Rica, July 23, 1936 (C.W.D. 9238), reached me. I recognized it as the same species. Both the Panamá and the Costa Rica collections differ from the species as described by Boedijn in the longer, more slender stalks and the larger number of branches, but such differences are exactly those of habit which characterize developmental forms of C. fruticulosa and which have been the occasion for such an unfortunate multiplication of synonyms in that species. Since the distinctive microscopic characters are the same, there is every reason to suppose that the New World and the Old World forms may be referred to the same species, but not to C. fruticulosa or any of its varieties. Since the original description is not readily available. I add tracings of Boedijn's drawings to the illustrations of the American collections.

COMATRICHA ELLISII Morgan.

This species was originally described from a specimen sent to Morgan from New Jersey by J. B. Ellis. Of the four collections in the University of Iowa collection, one was sent to Macbride by Ellis and may well be a portion of the type, two are from Ohio, determined by Morgan, and one is from southern Missouri, determined by Macbride. They all clearly represent the same species. The net is open, with few anastomoses, the spores are purplish gray, minutely punctate and 10–11 μ in diameter. In Lister's Mycetozoa in both the second and third editions, C. Ellisii is listed as a synonym of C. laxa, but Dr. Macbride believed it to be distinct. In my judgment, the disposition in the Mycetozoa is correct, all of the specimens studied being indistinguishable from small examples of C. laxa.

HEMITRICHIA MONTANA (Morg.) Macbr.

As originally described by Morgan (Jour. Cin. Soc. Nat. Hist. 18: 40. 1895) the color of this species was given as olive-vellow. In transferring the species from Hemiarcyria to Hemitrichia, Macbride (N. A. Slime-Moulds 208, 1899) rewrote the description, giving the general color as "whitish" and that of the peridium as "dull white." In the second edition (p. 266. 1922) the description was repeated without change, but it was noted that the species is "common throughout southwestern states to lower California." In spite of this latter statement, the only specimen available in the Iowa collection at the time THE MYXO-MYCETES went to press (1934) was a small fragment of the type. bearing a few sporangia from which all but the basal lobes of the peridium had disappeared and hence Macbride's description and comments were repeated with slight change of wording only. What is more serious, the color attributed to the species by Macbride was used as a key character. Recently an additional and better portion of the type has been found in the Morgan collection and the color reference proves to be quite misleading. The species is, indeed, somewhat paler than most of the other vellow species, but it is neither pallid nor whitish, but rather a clear, pale yellow, while the dense capillitium is rather deep ochraceous. Seven additional collections from three distinct localities in the vicinity of Mt. Rainier, Washington, made by Dr. D. B. Creager in August, 1928, prove to belong to this species. They have been unidentified all these years largely because I was misled by the reference to the color. In none is the capillitium lighter than in the type, but unopened sporangia are numerous, and there is some variation in the peridium. It is always yellow, but in some collections very thin and almost translucent, with iridescent reflections, while in others it is more opaque and appears duller.

G. Lister (Mycetozoa ed. 2: 226. 1911), presumably after having seen a portion of the type, decided that Morgan's species was based on an irregular form of *H. clavata* and this opinion is repeated in the third edition. Our now abundant material seems to show very clearly that this is not correct. *H. montana* differs from *H. clavata* not only in exterior form, but in peridial charac-

ters, spores and capillitium. It is even less like *L. clavata* than is *H. stipitata*, which Lister also combines with *clavata* and which has been very generally and quite inexcusably misunderstood in this country. In view of the confusion, it seems desirable to rewrite the description of *H. montana*:

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Sporangia gregarious or clustered, globose or obovate, sessile on a contracted base or short-stipitate, mostly 0.5–1 mm. in diameter before dehiscence, then up to 2 mm.; peridium thin, shining, translucent, or sometimes appearing dull and thicker from spore deposits, reticulate within under lens, breaking away in patches above but persisting as more or less petaloid lobes below; capillitium dense, elastic, bright ochraceous orange, becoming duller with age; elaters 6–8 μ in diameter, branching and anastomosing, with numerous free ends and vesicular enlargements; spirals five or six, rather close, bearing close-set minute spines; spores globose, bright ochraceous in mass, almost colorless under lens, minutely spinulose, $10-12~\mu$.

LICEA Schrad. Nov. Gen. Plant. 16: 1797, emend.

The original diagnosis of the genus referred to sessile species, with a thin wall, usually single, dehiscing irregularly and lacking capillitial threads among the spores. Four species are cited: L. Tubulina, expressly stated to be the same as Tubifera ferruginosa Gmel., L. clavata, very generally regarded as referring to a different phase of the same species, L. variabilis and L. pusilla, both of which names are still current. Since there has been some expression of doubt as to whether L. variabilis in Schrader's sense is the same form to which the name is today applied, it seems desirable to indicate L. pusilla as the type. The genus was accepted by Persoon (Syn. Meth. 195. 1801) in essentially Schrader's sense. Fries (Syst. Myc. 3: 193. 1829) revised the genus, dividing it into the "tribes" Tubulina (i.e. Tubifera), Serpularia, for the more or less plasmodiocarpous forms, and Phelonitis for two minute sporangiate species. L. pusilla he relegates to Physarum as P. Licea.

In his earlier work, Rostafinski (Versuch 4. 1873) recognizes Licea and Tubulina as distinct genera and maintains this in his monograph (Sluz. 201–202. 1875) citing two species in Licea, L. flexuosa Pers. and L. variabilis Schrad. Licea pusilla he

makes the type and sole representative of his new genus Protoderma (Sluz. 90. 1875). Some years later Wingate established the genus Orcadella (Proc. Acad. Nat. Sci. Phil. 1889: 280) to accommodate a minute species which is essentially a stalked Licea with a lid, neither character, however, being entirely con-Massee (Mon. 35. 1892) recombined Licea and Tubuling, under the latter name, adding to them Lindbladia. Shortly thereafter Hymenobolina Zukal (Oesterr, Bot, Zeitschr, 43: 133. 1893) and Kleistobolus Lippert (Verh. Zool.-Bot. Ges. Wien 44: 70. 1894) were founded to accommodate two small species which are essentially sessile Liceas with lids. Gilbert (Univ. Iowa Stud. Nat. Hist. 16: 153. 1934) described as Hymenobolina pedicellata a species which is essentially a stalked Licea without a lid, recognizing that it did not fit into either Licea or Hymenobolina as then delimited. Very recently, Hagelstein (Mycologia 1942) has proposed uniting Kleistobolus and Hymeno-34: 258. bolina with Orcadella. I have long been of the opinion, not only that these three genera are based on inadequate distinctions, but that they should be united with Licea. The presence or absence of a stalk is not usually regarded as a generic difference and the presence or absence of a definite lid is scarcely of greater significance. The latter character, it is true, is used to separate Craterium from Physarum and, with the addition of a typical plasmodiocarpous fructification, Perichaena from Ophiotheca. Neither of these instances affords a particularly good precedent. In the former case, it is admittedly artificial and justified, not because it is believed to represent any fundamental distinction, but purely by the convenience of separating a fairly coherent group of species from a large and complex genus. In the latter case, even with the additional character, it is not regarded as significant, and the Lister monograph, with much justification, combines the two genera. In my experience, the presence of a lid, while constant in Kleistobolus, is far less so in Hymenobolina parasitica or Orcadella operculata, although the last-named species is much less common with us than the other two and hence I have had less opportunity to observe it. Likewise, the stalked character in Orcadella and in Hymenobolina pedicellata is admittedly inconstant.

I therefore propose that the genus *Licea* be emended to include all Myxomycetes with separate, limeless, sporangiate or plasmodiocarpous fructifications, sessile or stalked, dehiscent irregularly, by plates or by lids and lacking a massive hypothallus and capillitium, other than the finger-like protrusions from the inside of the cap in *Kleistobolus*. As thus emended, the genus is close to *Tubifera*, the latter differing in its massive hypothallus upon which the sporangia are closely packed or heaped, characteristically forming a pseudoaethalium.

The following transfers are proposed: Licea operculata (Wing.) comb. nov.; Licea parasitica (Zukal) comb. nov.; Licea pedicellata Gilbert, comb. nov. The transfer of *Hymenobolina pedicellata* to *Licea* under Dr. Gilbert's name is with his consent and approval, expressed some years ago.

Since Licea pusilla Schrad. is already in existence, I propose for Kleistobolus pusillus the combination Licea Kleistobolus nom. nov.

The family Liceaceae should be enlarged to include *Tubifera*, since the massive hypothallus and pseudoaethalial habit of the latter genus, while useful generic characters, do not deserve to be considered as a sufficient basis for segregation into a distinct family. *Alwisia* and *Liceopsis* need further study before their position can be more than tentatively fixed.

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In the article cited, Hagelstein objects to considering in taxonomic work results secured in cultures "until fully substantiated." Just what this means is not clear. Certainly all will agree that it is highly undesirable to publish any work until reasonable care has been taken to make sure that it is correct. But if it be intended to imply that only Myxomycetes collected in the open are to be regarded as a satisfactory basis for taxonomic study of the group, I must emphatically dissent. Some cultural developments, it is true, are highly aberrant; so are many fruitings found in the open. I have been bringing slime molds to fructification in moist chambers for many years, and I have seen so many different species come to perfect fruiting under such circumstances that I have come to regard such cultures as an invaluable adjunct to the study of the field material. Not only are the fruitings frequently more perfect than those

collected outside but a number of species, especially minute ones rarely seen in the field and previously supposed to be uncommon, have been shown to be abundant and widely distributed. Among such are Licea parasitica and L. Kleistobolus mentioned above, as well as Licea biforis, Clastoderma Debaryanum, Comatricha fimbriata and Echinostelium minutum. Furthermore, observation of developing fructifications under such circumstances often vields information of considerable significance. Thus it seems perfectly true that some species, of which Licea pedicellata and L. operculata are examples, ordinarily arise from small plasmodia, giving rise to one or a few fructifications. What I regard as more significant is that several of these small species, notably L. minima, L. parasitica and L. Kleistobolus, have rather extensive plasmodia in the substratum, but the plasmodia do not emerge to the surface as in more highly developed species, but, when ready to fruit, send out through the pores of the substratum individual droplets of protoplasm, each of which will form a separate sporangium. Emergence, in these species, is clearly a part of the fruiting process.

PHYSARUM BETHELII Macbr. ex List.

Sturgis (Colo. Coll. Pub. Sc. ser. 12: 439. 1913) and Lister (Mycetozoa ed. 3. 36. 1925) concur in regarding this species as a variety of P. viride (Bull.) Pers. Brandza, however, regards it as distinct (Bull. Soc. Myc. Fr. 44: 256. 1929). On the basis of the material available for study I cannot agree that Bethelii is no more than a variety of viride. P. viride is, it is true, highly variable, as is often the case with common and widely distributed species, nevertheless I find nothing in our abundant material which I should regard as merging into Bethelii. On the other hand, certain specimens determined as P. Bethelii, or as P. viride var. Bethelii, seem to me to represent viride and to be scarcely worthy of varietal segregation. In what I take to be the type collection of P. Bethelii, of which Lister's plate 200a is an accurate representation, the stipe is short, the peridium is nearly limeless and iridescent blue, the lower portion remaining as a cup, the capillitium is paler than is usual in viride and arises

from the inserted base of the stipe in such a way as almost to suggest a columella, and the spores are slightly larger and more distinctly warted than those of *viride*.

In addition to the Colorado collection, presumed to be part of the type, we have a small, but typical gathering from Washington.

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STATE UNIVERSITY OF IOWA, IOWA CITY

NOTES AND BRIEF ARTICLES

"THE ADVENTURE OF THE ARDENT MYCOLOGIST"

To some of us mycology is a profession or a semi-profession. To others, who have a real profession, mycology or mycophagy is pursued merely as a hobby. This is true of a recent caller in our office, Mr. Percival Wilde, well known author and playwright, who during his periods of relaxation plays with the fungi. In his latest book "Tinsley's Bones" he has devoted a chapter to the above title in which he depicts some of the idiosyncrasies of an ardent and rather absent minded, which is to say, typical mycologist. Professional mycologists during their periods of relaxation would very much enjoy reading this, as well as the remainder of the book.—Fred J. Seaver.

OCCURRENCE OF GONATORRHODIELLA HIGHLEI IN NOVA SCOTIA AND NEW BRUNSWICK

In his recent paper (Mycologia 33: 178–187. 1941.), Ayers reported Gonatorrhodiella Highlei A. L. Smith growing in association with Nectria coccinea (Pers. ex Fries) Fries and the woolly beech scale (Cryptococcus Fagi (Baer.)) on diseased American beech (Fagus grandifolia Ehrh.) in Maine. Therefore, it is thought of interest to record that G. Highlei (determinations checked recently by Ayers) occurred under similar circumstances in affected beech stands throughout Nova Scotia and in Albert County, New Brunswick, during the summers of 1930, 1931, and 1932.

In answer to a question addressed early in 1942 to R. E. Balch of the Dominion Entomological at Fredericton, N. B., he replied as follows. "... The brown mold can, I think, be found wherever heavy infestations of the scale occur. ... It has not been noted on scale-infested trees as invariably as the *Nectria*. ... I know that the mold occurs at Fredericton, but I cannot be sure that it has been collected north of here."—John Ehrlich.

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Butler, Ellys, T., see Wodehouse.

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Hardison, John R., 2702 Summitview Ave., Yakima, Wash.

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Lefebvre, Dr. Ç. L., U. S. Horticultural Field Station, Beltsville, Md. Martin, Dr. Ella May, Biology Department, Hood College, Frederick, Md.

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Morse, Miss Elizabeth E., Hotel Claremont, Berkeley, Calif.

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FINANCIAL STATEMENT

December 31, 1940-December 31, 1941

Balance on hand Dec. 31, 1940	
Cash	
Government Bonds	20
Savings account (as of 1939)	50
Receipts	
Annual dues in part 1940, 1941	184
Interest on Savings account (since 1939)	1
Expenditures	
New York Botanical Garden for Mycologia \$1503.00	
Returned checks	
Postage and envelopes	
Secretarial help	
Yearbook notices	
New York Botanical Garden for yearbook 112.00	
Mimeographing	
Telephone and telegraph 5.07	
Programs for Dallas meeting	
Sect'y's travelling exp. to Phila 59.14	
Biologists smoker	
State tax on Bank Deposits	
\$1815.20	-
Balance on hand Dec. 31, 1941	
Cash \$ 766.92	
Government Bonds	
Savings account	

(Signed) J. N. Couch, Secretary-Treasurer

\$3300.69 \$3300.69

Examined and found correct:

Delbert Swartz, Chairman of Auditing Committee
Dallas, Texas, Dec. 29, 1941

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